INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

ProQuest Information and Learning
300 North Zeeb Road, Ann Arbor, MI 48106-1346 USA
800-521-0600

UMI®

Biodiversity Priorities and Conservation Decision-Making:

The Role of Spatial Scale, Irreplaceability and Vulnerability in Guyana

Karen Suzanne Richardson
Department of Geography
McGill University
April 2000

A thesis submitted to the Faculty of Graduate Studies and Research
in partial fulfilment of the requirements of the degree of Doctor of Philosophy

National Library of Canada

Acquisitions and Bibliographic Services

395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque nationale du Canada

Acquisitions et services bibliographiques

395, rue Wellington
Ottawa ON K1A 0N4
Canada

0-612-64651-3

ABSTRACT

The application of systematic conservation decision-making methodologies requires data on the spatial distribution of the elements of biodiversity. When a decision on where to put a protected area to conserve biodiversity must be made at a given time, the decision must be based on the best data available. But, adequate data are often lacking. This thesis examines the use of surrogate measures of biodiversity in conservation decision-making in Guyana, South America. The study looks at different surrogate measures and their influence on the selection of priority biodiversity sites for conservation. Surrogate measures at the ecosystem and species level are examined. The research shows that measures from different hierarchical levels produce different outcomes on the location of sites, however measures at the ecosystem-level appear to capture most of the known species distributions. The thesis examines cross-taxon congruency and shows that the spatial scale of analysis influences patterns of congruency for different taxonomic groups. The influence of spatial scale is also examined for various measures of biodiversity and it is shown that variability of species richness decreases with increased selection unit size. Finally, an index of vulnerability is used to prioritise conservation of sites in Guyana based on urgency, which is defined by two different threats: agriculture and forestry. This thesis adopts a conceptual framework based on data-driven, efficient, flexible and transparent methodologies and uses it to demonstrate how a network of protected areas might be established in Guyana that uses the most comprehensive data available on biodiversity. The thesis concludes by presenting a protocol for conservation decision-making that incorporates some of the theoretical principles identified by this work as important for measuring biodiversity and planning a protected area network.

RÉSUMÉ

L'application de systèmes d'aide à la prise de décisions en matière de conservation systématiques se fonde sur des données sur la répartition spatiale des éléments de la diversité biologique. La décision de donner le statut de zone protégée afin de préserver la biodiversité doit s'appuyer sur les meilleures données disponibles. Cette thèse s'intéresse aux mesures de substitution de la biodiversité dans la prise de décisions en matière de conservation en Guyane (Amérique du Sud). L'étude porte sur différentes mesures de substitution de la biodiversité et sur leur influence sur l'emplacement des sites prioritaires en matière de conservation. La recherche démontre que les mesures provenant de différents niveaux hiérarchiques donne différents résultats au titre de l'emplacement des sites, même si les mesures touchant l'écosystème semblent prendre en compte la plupart des espèces connues. La thèse examine la congruence des taxons et démontre que l'échelle spatiale de mesure influe sur la congruence des différents groupes taxonomiques. L'influence de l'échelle est également étudiée par rapport à différentes mesures de la biodiversité, analyse qui révèle que la variabilité diminue avec l'augmentation de la taille de la sélection. Enfin, un indice de la vulnérabilité est utilisé pour établir les priorités en matière de sites en Guyane compte tenu de l'urgence, définie par deux menaces différentes : l'agriculture et l'exploitation forestière. Cette thèse adopte un cadre conceptuel s'appuyant sur des méthodes transparentes, souples, efficaces et fondées sur les données qui permettent de démontrer comment un réseau de zones protégées peut être établi en Guyane à l'aide de données les plus complètes possible sur la biodiversité. En conclusion, la thèse propose un protocole de prise de décision en matière de conservation qui intègrent certains des principes théoriques identifiés ultérieurement et qui jouent un rôle important dans la mesure de la biodiversité et la planification d'un réseau de zones protégées.

FOREWORD

This thesis contributes to knowledge and theory on conservation decision-making using data from Guyana, South America. The study examines several surrogate measures of biodiversity used to identify priority biodiversity sites including environmental domains, vegetation classes and species distributions. This research is the first to compare the location of priority biodiversity sites for the same area (Guyana) using the same decision-making framework, while varying the surrogate measures of biodiversity. It contributes a new understanding of: (a) the patterns of climate, terrain and substrate in Guyana, and how those patterns, once translated into classifications, perform in the selection of priority biodiversity sites. (b) Differences in species-based surrogate measures of biodiversity, including species richness, restricted range, irreplaceability and cross-taxon surrogacy patterns and their performance in the selection of priority biodiversity sites. Although there have been a few studies on the usefulness of species-based surrogates, the surrogacy values of irreplaceability sets have never been assessed and the differences in location of priority biodiversity sites for different measures have never been compared. (c) The influence of selection unit sizes on the observed spatial patterns of species richness, the location of priority biodiversity sites, and the ability of indicator taxa to act as surrogates for one another. In addition, the influence of spatial scale is examined by testing whether patterns of species richness and irreplaceability are predictable with changes in the selection unit size. (d) Differences between priority biodiversity sites and priority conservation site, those sites that incorporate some assessment of the urgency for conservation.

The conservation decision-making framework adopted and applied in this thesis is an original adaptation of several systematic conservation decision-making methodologies. Likewise, the protocol on identifying high priority conservation sites in Guyana is original. Both the protocol and conceptual framework developed in the thesis contribute to ‘real-world” conservation planning and can be used for protected area planning in any location, at any scale.

This study differs from previous studies and research on conservation decision-making in several ways. First, this study uses a measure of irreplaceability rather than species richness or endemism to compare the effectiveness of different surrogate measures of biodiversity. Second, this study varies the size of the selection unit and examines the impact of different selection unit sizes on the location of priority sites, using the same dataset. Thirdly, different indices of vulnerability are used and compared to identify priority conservation sites. Lastly, data and results on different biodiversity measures and surrogate efficiency presented in this thesis are the first for any tropical area in South America and hence, are important for comparison with African, European and North American results.

ACKNOWLEDGEMENTS

I would like to thank a number of people for their inspiration and support throughout this thesis. I am truly grateful to my supervisor, Thom Meredith for his encouragement, patience and support. Thom provided much guidance on structure, content, and strategies on how to finish from Australia. I am also indebted to my committee members, John Lewis and Theo Hills, for their support and feedback. Theo inspired me to work on Guyana as a case study and provided many hours of stories and facts on Guyana from his amazing wisdom and knowledge of the country. Gordon Ewing stimulated me to consider some of the questions on spatial scale and helped with a few administrative problems, for which I am thankful.

Vicki Funk at the Smithsonian Institution provided me with all the species data from the Smithsonian's collection. She also provided advice and guidance throughout every stage of research and in every city (Georgetown, Washington, Montreal and Brisbane). She proved to be invaluable as an expert on Guyana. And provided the best babysitting services outside of the family.

This thesis would not have been possible without support from the Global Environment Facility-World Bank NPAS Project in Guyana, for which I worked as a consultant. Claudia Alderman, Kathy MacKinnon, Lorretta Sprissler, Kathy Mikitin, Nathalie Johnson and Ken Newcombe at the World Bank assisted me in more ways than I can count and I am truly grateful. Kathy MacKinnon helped to point me in the right direction many times and provided me with an introduction to Bob Pressey.

In Guyana, I would like to thank the Centre for Biodiversity at the University of Guyana and especially Naseem Nassir and Tom Hollowell (in Washington and Guyana) for helping with ArcView layers and data in general. The Government of Guyana, in particular Navin Chanderpaul, provided much information and fruitful

discussions on protected areas in Guyana. Lastly, many thanks to Malcolm and Margaret Chan-a-Sue who flew us around the country safely, always gave us something to talk about and looked after us in Guyana.

This work would not have been possible without the generosity of Bob Pressey at New South Wales National Parks and Wildlife Service in Armidale and his team of researchers, Tom Barrett and Matt Watts, who provided me with C-Plan and always answered my calls for help. I am truly grateful for the opportunity to have been a 'beta-tester' of C-Plan. I am also indebted to Simon Ferrier at NSW NPWS for being an inspiration and providing many hours of discussion and guidance on ways to improve biodiversity surrogates. Simon was the best officemate during his sabbatical at UQ and provided endless enthusiasm.

I would like to thank my colleagues at McGill, Tom Fletcher, John Hull, Scot Nickels and T.C Chang for their support, humour and many dinners. Jennifer Slinger, Craig Lapp, Erin O'Brien and Wynet Smith provided an endless teapot and much needed distractions during various phases.

In Australia, I would like to thank Craig Moritz at the Centre for Conservation Biology and zoology department at the University of Queensland for providing me with an office and access to the resources I needed. The WH Byran Research Centre at the University of Queensland also provided me with many resources for which I am grateful.

Anita Smyth, Judy O'Neil and Elsie Krebs kept the pressure on me to finish in Australia and always gave me a reason to smile and go on with my work when motherhood looked likely to win over academia.

My siblings, Eric, Celia, Eva and Alan, and in-laws, Ciana and Bruce were always supportive and ready to pitch in and help out. A special thanks to Alan Richardson for teaching me about super carnivores and the importance of large mammals in conservation.

My father, John, and Edie provided endless support. They helped us out with almost everything from meals to computers. I am very extremely grateful for their support and love throughout this thesis.

I could not have completed this thesis without the support from my mother, Astrid, who also gave up time to help me through it by being everything from an expert babysitter and cook, to mentor. Her love and dedication was especially appreciated in the final months.

My son, Alexander deserves a big thanks for surviving his first year of life near or under my computer and not destroying it. He helped sort my references and provided many smiles during the process.

Finally, this thesis would never have seen the light of day if it weren't for my husband, Roussos who saw me through every step. His confidence that I would finish and emotional support allowed me juggle many things at once. I owe him more than I can say.

TABLE OF CONTENTS

Page

ABSTRACT i

RESUME ii

FOREWORD .... iii-iv

ACKNOWLEDGEMENTS .... v-viii

TABLE OF CONTENTS .... viii-xiii

LIST OF FIGURES AND TABLES .... xiv-xviii

LIST OF ACROYMS xix

Chapter 1: General Introduction 1

1.1 Introduction 1

1.2 Statement of Problem, Aims and Objectives 5
    1.2.1 Statement of Problem 5
    1.2.2 Aims and Objectives 6

Chapter 2: Guyana: The Case Study 10

2.1 National Context 10
    2.1.1 Geographical Situation 10
    2.1.2 Demography 10
    2.1.3 The Economy 12
        2.1.3.1 Agriculture and Fisheries 14
        2.1.3.2 Mining 14
        2.1.3.3 Forestry 15
        2.1.3.4 Wildlife Trade 17

2.2 Biophysical Parameters 18
    2.2.1 Climate 18
    2.2.2 Topography 18
        2.2.2.1 The Low Coastal Plains 19
        2.2.2.2 The Sandy Rolling Lands 19
        2.2.2.3 The Highland/Pakaraima Region 19
        2.2.2.4 The Pre-Cambrian Lowland 19
    2.2.3 Hydrology 20
    2.2.4 Geology and Soil 20

2.3 Biogeography 22
    2.3.1 Biogeographical Provinces and Communities 22
    2.3.2 Vegetation Map 25
    2.3.3 Flora 26
    2.3.4 Fauna 28
    2.3.5 Status of Flora and Fauna 28
        2.3.5.1 Status of Plants 28
        2.3.5.2 Status of Animals 29

2.4 Conservation Actions 29
    2.4.1 Protected Areas 29
        2.4.1.1 Kaieteur Falls National Park 30
        2.4.1.2 Iwokrama Rainforest Project 31
    2.4.2 Proposed Conservation Actions 32

2.5 Conclusions 33

Chapter 3: Literature Review and Conceptual Framework for Conservation Decision-Making

3.1 Introduction 35

3.2 Patterns of Biodiversity Distribution 36
    3.2.1 Patterns of Biodiversity at the Global Scale 37
    3.2.2 Patterns of Biodiversity at the Continental Scale 38
    3.2.3 Patterns of Biodiversity at the Environmental Gradient Scale . 39
    3.2.4 Patterns of Biodiversity on Islands 40
    3.2.5 Patterns of Biodiversity at a Local Scale 41

3.3 Surrogate Measures of Biodiversity 42
    3.3.1 Vegetation Mapping 42
    3.3.2 Environmental Domains 43
    3.3.3 Estimated Species Data 44
        3.3.3.1 Predictive Modelling of Species 45
        3.3.3.2 Indicator Taxonomic Groups 45
        3.3.3.3 Data Sources 46

3.4 Methods for Selecting Protected Areas 47
    3.4.1 Selection Algorithms 49
    3.4.2 Gap Analysis 50
    3.4.3 Irreplaceability 51

3.5 Role of Spatial Scale 52
    3.5.1 Scaling Theory 53
    3.5.2 Patterns and Spatial Scale 54

3.6 Evaluating Options for Biodiversity Conservation 57

3.7 Conceptual Framework for Conservation Decision-making.................. 59

Chapter 4: Biophysical Measurement of Biodiversity in Guyana 60

4.1 Introduction 60
    4.1.1 Biophysical Biodiversity Surrogates 63
        4.1.1.1 Climatic and other Abiotic Environmental Variables 63
        4.1.1.2 Environmental Domains 64
        4.1.1.3 Vegetation Classifications 65
    4.1.2 Irreplaceability 65
    4.1.3 Priority Biodiversity Site Selection 66
        4.1.3.1 Selection Algorithms 66
        4.1.3.2 Conservation Targets 67

4.2 Methods 67
    4.2.1 Data Collection.. 68
        4.2.1.1 Digital Elevation Model (topography) 68
        4.2.1.2 Climate Records.. 72
        4.2.1.3 Temperature and Rainfall Measurements 75
        4.2.1.4 Lithology and Soil Fertility 76
        4.2.1.5 Vegetation... 76
    4.2.2 Environmental Domains Classification 76
    4.2.3 Irreplaceability 79
    4.2.4 Priority Biodiversity Site Selection 80

4.3 Results.. 81
    4.3.1 Climate... 81
    4.3.2 Topography 85
    4.3.3 Lithology.. 85
    4.3.4 Vegetation 86
    4.3.5 Environmental Domains 87
    4.3.6 Irreplaceability 87
    4.3.7 Selection of Priority Biodiversity Sites 96
    4.3.8 Difference in Targets... 106

4.4 Discussion 108

Chapter 5: Species as a Measure of Biodiversity..................................... 116

5.1 Introduction 116
    5.1.1 Species Survey Data.. 118

    5.1.2 Species-based Measures of Biodiversity 119

5.1.2.1 Species Richness 119
5.1.2.2 Species Restrictness 120
5.1.2.3 Hotspots 121
5.1.2.4 Cross-Taxon Congruency 122
5.1.2.5 Congruency between Restrictedness and Species Richness 123
5.1.3 Selection of Priority Biodiversity Sites Using Species-Based Data 124
5.1.3.1 Complementarity 124
5.1.3.2 Irreplaceability 125

5.2 Methods 126
5.2.1 Data Collection 126
5.2.2 Modelling 128
5.2.3 Species Richness 130
5.2.4 Restricted Range 132
5.2.5 Hotspots 133
5.2.6 Irreplaceability 134
5.2.7 Priority Biodiversity Site Selection 134
5.2.8 Cross-Taxon Surrogacy 135
5.2.9 Comparison with Environmental Domains and Vegetation Classes 136

5.3 Results 137
5.3.1 Species Richness Distribution 137
5.3.1.1 Full Dataset 137
5.3.1.2 Reduced Dataset 137
5.3.2 Restricted Range Distribution 140
5.3.3 Species Richness Hotspots 140
5.3.4 Restricted Range Hotspots 140
5.3.5 Irreplaceability Values 145
5.3.6 Priority Biodiversity Site Selection 145
5.3.6.1 Species Richness 145
5.3.6 2 Summed Irreplaceability 150
5.3.7 Cross-Taxon Surrogacy 150
5.3.8 Comparison with Environmental Domains and Vegetation Classes 153

5.4 Discussion 167

Chapter 6: Influence of Spatial Scale 170

6.1 Introduction 170
6.1.1 Species Richness 173
6.1.2 Efficiency and Overlap of Selection Units 174
6.1.3 Cross-Taxon Surrogacy 175

6.2 Methods 175
    6.2.1 Species Richness 176
    6.2.2 Selection of Priorate Biodiversity Sites 176
    6.2.3 Cross-Taxon Surrogacy 177

6.3 Results 178
    6.3.1 Species Richness 178
    6.3.2 Selection of Priority Biodiversity Sites 179
    6.3.3 Cross-Taxon Congruency 193

6.4 Discussion 210
    6.4.1 Species Richness 211
    6.4.2 Priority Biodiversity Sites 212
    6.4.3 Cross-Taxon Congruency 213

Chapter 7: Planning for Vulnerability, Retention and Persistence 215

7.1 Introduction 215
    7.1.1 Threats to Biodiversity 217
    7.1.2 Retention and designing for Long-term Persistence of Biodiversity Features 219
    7.1.3 Trade-offs between Biodiversity and Other Economic Activities 222

7.2 Methods 223
    7.2.1 Vulnerability Index based on Slope and Soil Fertility 223
    7.2.2 Vulnerability Index based on Proximity to State Forests 224
    7.2.3 Selection of Priority Conservation Sites 225

7.3 Results 225
    7.3.1 Vulnerability Index based on Slope and Soil Fertility 225
    7.3.2 Priority Conservation Sites based on Vulnerability Index derived from Slope and Soil Fertility and Summed Irreplaceability 225
    7.3.3 Vulnerability Index based on Proximity to State Forest 228
    7.3.4 Priority Conservation Sites based on Vulnerability Index derived from Proximity to the State Forest and Summed Irreplaceability 228
    7.3.5 Overlap in Priority Conservation Sites 233

7.4 Discussion 233
    7.4.1 Protocol for Retention and persistence of Biodiversity in Guyana 234

Chapter 8: Summary and Conclusions 239

8.1 Introduction 239

8.2 Main Findings 239
  8.2.1 Measures of Biodiversity 240
  8.2.2 Criteria and Representation Targets 241
  8.2.3 Minimum Set Selection Algorithms 242
  8.2.4 Appropriate Spatial Scale 243
  8.2.5 Evaluation Mechanisms 244

8.3 Conclusions 244

References 246

Appendix 1: Example of Database of Species Collections 266

LIST OF FIGURES AND TABLES

Figures page

Figure 1: Location of Guyana 11
Figure 2: Administrative Regions of Guyana 13
Figure 3: State Forest in Guyana 16
Figure 4: Rivers and Streams of Guyana 21
Figure 5: Lithology of Guyana 23
Figure 6: Vegetation Map of Guyana 27
Figure 7: Cost-Benefit of Protection 58
Figure 8: Elevation of Guyana 69
Figure 9: Elevation in 300m Intervals 70
Figure 10: Terrain Ruggedness 71
Figure 11: Rainfall Stations across Guyana 73
Figure 12: Temperature Stations across Guyana 74
Figure 13: Soil Fertility of Guyana 77
Figure 14: Mean Annual Temperature (C) 81
Figure 15: Mean Annual Rainfall (mm) 84
Figure 16: Rainfall for October (mm) 86
Figure 17a: 228 Environmental Domains 88
Figure 17b: 100 Environmental Domains 89
Figure 17c: 34 Environmental Domains 90
Figure 18a: Summed Irreplaceability for 228 Domains 91
Figure 18b: Summed Irreplaceability for 100 Domains 92
Figure 18c: Summed Irreplaceability for 34 Domains 93
Figure 18d: Summed Irreplaceability for Vegetation Classes 94
Figure 19: (a) Minimum Set of Sites with 228 Domains 15 % Target; 98
(b) Minimum Set of Sites with 228 Domains 3 Occurrences Target; 99
(c) Minimum Set of Sites with 100 Domains 15 % Target; 100
(d) Minimum Set of Sites with 100 Domains 3 Occurrences Target; 101
(e) Minimum Set of Sites with 34 Domains 15 % Target; 102
(f) Minimum Set of Sites with 34 Domains 3 Occurrences Target; 103
(g) Minimum Set of Sites with Vegetation Classes 15 % Target; 104
(h) Minimum Set of Sites with Vegetation Classes 3 Occurrences Target. 105
Figure 20: (a) Feature Accumulation Curve 228 Domains;
(b) Feature Accumulation Curve 100 Domains 109
(c) Feature Accumulation Curve 34 Domains;

(d) Feature Accumulation Curve Vegetation Classes 110
Figure 21: (a) Comparison of Areas 228 Domains;
(b) Comparison of Areas 100 Domains 111
(c) Comparison of Areas 34 Domains;
(d) Comparison of Areas Vegetation Classes 112
Figure 22: Collecting Localities in Guyana 129
Figure 23: Example of Recorded and Predicted Distribution of a Species 131
Figure 24: Species Richness using Dataset of 5,123 Species 138
Figure 25: Species Richness using Dataset of 320 Species 139
Figure 26: Restricted Range using Dataset of 320 Species 141
Figure 27: Species Richness Hotspots 142
Figure 28: Restricted Range Hotspots 143
Figure 29: Summed Irreplaceability Target of 3 Occurrences 148
Figure 30: Priority Biodiversity Sites Selected using Species Richness 149
Figure 31: Priority Biodiversity Sites Selected using Summed Irreplaceability 151
Figure 32: (a) Species Accumulation Curves when Birds are the Target Group; (b) Species Accumulation Curves when Understorey Trees are the Target Group; 154
(c) Species Accumulation Curves when Ferns are the Target Group; (d) Species Accumulation Curves when Amphibians are the Target Group 155
(e) Species Accumulation Curves when Emergent Trees are the Target Group; (f) Species Accumulation Curves when Legumes are the Target Group 156
(g) Species Accumulation Curves when Mammals are the Target Group; (h) Species Accumulation Curves when Melastomes are the Target Group 157
(i) Species Accumulation Curves when Orchids are the Target Group; (j) Species Accumulation Curves when Sedges are the Target Group 158
Figure 33: (a) Comparison of Areas when Birds are the Target Group; (b) Comparison of Areas when Understorey Trees are the Target Group 159
(c) Comparison of Areas when Ferns are the Target Group; (d) Comparison of Areas when Amphibians are the Target Group 160
(e) Comparison of Areas when Emergent Trees are the Target Group; (f) Comparison of Areas when Legumes are the Target Group 161
(g) Comparison of Areas when Mammals are the Target Group; (h) Comparison of Areas when Melastomes are the Target Group 162

(i) Comparison of Areas when Orchids are the Target Group; (j) Comparison of Areas when Sedges are the Target Group 163
Figure 34: (a) Species Accumulation when 228 Domains are used to Select Priority Sites; (b) Species Accumulation when 100 Domains are used to Select Priority Sites 164
: (c) Species Accumulation when 34 Domains are used to Select Priority Sites; (d) Species Accumulation when Vegetation Classes are used to Select Priority Sites 165
Figure 35: Accumulation of Vegetation Classes when Plants are used to Select Priority Sites 166
Figure 36a: Species Richness at a Grid Size of 16 km^2 180
Figure 36b: Species Richness at a Grid Size of 64 km^2 181
Figure 36c: Species Richness at a Grid Size of 256 km^2 182
Figure 36d: Species Richness at a Grid Size of 1,024 km^2 183
Figure 36e: Species Richness at a Grid Size of 4,096 km^2 184
Figure 36f: Species Richness at a Grid Size of 16,384 km^2 185
Figure 37: Coefficient of Variation of Richness for Different Grid Sizes 186
Figure 38a: Selected Priority Sites at 16 km^2 187
Figure 38b: Selected Priority Sites at 64 km^2 188
Figure 38c: Selected Priority Sites at 256 km^2 189
Figure 38d: Selected Priority Sites at 1,024 km^2 190
Figure 38e: Selected Priority Sites at 4,096 km^2 191
Figure 38f: Selected Priority Sites at 16,384 km^2 192
Figure 39: (a) Comparison of Areas when Birds are the Target Group at 64 km^2; (b) Species Accumulation Curves when Birds are the Target Group at 64 km^2 195
(c) Comparison of Areas when Understorey Trees are the Target Group at 64 km^2; (d) Species Accumulation Curves when Understorey Trees are the Target Group at 64 km^2 196
(e) Comparison of Areas when Ferns are the Target Group at 64 km^2; (f) Species Accumulation Curves when Ferns are the Target Group at 64 km^2 197
(g) Comparison of Areas when Amphibians are the Target Group at 64 km^2; (h) Species Accumulation Curves when Amphibians Trees are the Target Group at 64 km^2 198
(i)Comparison of Areas when Emergent Trees are the Target Group at 64 km^2; (j) Species Accumulation Curves when Emergent Trees

are the Target Group at 64 km^2 199
(k) Comparison of Areas when Legumes are the Target Group at 64 km^2; (l) Species Accumulation Curves when Legumes are the Target Group at 64 km^2 200
(m) Comparison of Areas when Mammals are the Target Group at 64 km^2; (n) Species Accumulation Curves when Mammals are the Target Group at 64 km^2 201
(o) Comparison of Areas when Melastomes are the Target Group at 64 km^2; (p) Species Accumulation Curves when Melastomes are the Target Group at 64 km^2 202
(q) Comparison of Areas when Orchids are the Target Group at 64 km^2; (r) Species Accumulation Curves when Orchids are the Target Group at 64 km^2 203
(s) Comparison of Areas when Sedges are the Target Group at 64 km^2; (t) Species Accumulation Curves when Sedges are the Target Group at 64 km^2 204
Figure 40: (a) Comparison of Areas when Birds are the Target Group at 256 km^2; (b) Comparison of Areas when Understorey Trees are the Target Group at 256 km^2 205
(c) Comparison of Areas when Ferns are the Target Group at 256km^2; (d) Comparison of Areas when Amphibians are the Target Group at 256km^2 206
(e) Comparison of Areas when Emergent Trees are the Target Group at 256 km^2; (f) Comparison of Areas when Legumes are the Target Group at 256 km 207
(g) Comparison of Areas when Mammals are the Target Group at 256 km^2; (h) Comparison of Areas when Melastomes are the Target Group at 256 km^2 208
(i)Comparison of Areas when Orchids are the Target Group at 256 km^2; (j) Comparison of Areas when Sedges are the Target Group at 256 km^2 209

Figure 41: Vulnerability Index based on Soil Fertility and Slope 226
Figure 42: Ranking of Grid Cells based on Summed Irreplaceability and Vulnerability Derived from Soil Fertility and Slope 227

Figure 43: Selected Priority Sites based on Summed Irreplaceability and Vulnerability Derived from Soil Fertility and Slope 229
Figure 44: Vulnerability Index based on Proximity to State Forest 230
Figure 45: Ranking of Grid Cells based on Summed Irreplaceability and Vulnerability due to Proximity to State Forest 231
Figure 46: Selected Priority Sites based on Summed Irreplaceability and Vulnerability due to Proximity to State Forest 232

Tables

Table 1 The Administrative regions of Guyana 12
Table 2 Biogeographical provinces and biotic communities of Guyana 24-25
Table 3 Summary of Climatic Data 83
Table 4 Spearman Rank correlation of summed irreplaceability 96
Table 5 Comparison of minimum sets 106
Table 6 Overlap in grid cells for minimum set runs using a target of 15 % and 3 occurrences 107
Table 7 Number of species and genera used for each taxonomic group 128
Table 8 Overlap of species richness hotspots 144
Table 9 Overlap of restricted range hotspots 146
Table 10 Overlap of richness and restricted range hotspots 147
Table 11 Percent of grid cells required to represent all species in the reduced dataset when priority sites are selected using environmental domains or vegetation classes 167
Table 12 The percent of grid cells required to represent species and index of efficiency for different selection unit sizes 179
Table 13 Ranking of vulnerability index based on slope and soil fertility 224
Table 14 Steps in the protocol for establishing a protected area network in Guyana 236-238

LIST OF ACRONYMS

BDG	Biological Diversity of the Guianas Program
CI	Conservation International
CITES	Convention on the International Trade of Endangered Species
CRES	Centre for Resource and Environmental Studies
CGIAR	Consultative Group on International Agricultural Research
DEM	Digital Elevation Model
EBA	Endemic Bird Areas
ESRI	Environmental Systems Research Institute
FAO	Food and Agriculture Organisation
GAHEF	Guyana Agency for Health Sciences Education, Environment and Food Policy
GCV	Generalised cross-validation
GIS	Geographic Information System
GDP	Gross Domestic Product
GNP	Gross National Product
Ha.	Hectares
IUCN	The World Conservation Union
NEAP	National Environmental Action Plan
NSW NPWS	New South Wales National Parks and Wildlife Service
OTA	Office of Technology Assessment
Pop.	Population
UNDP	United Nations Development Program
USAID	United States Overseas Aid Agency
USGS	United States Geological Service
WCMC	World Conservation Monitoring Center

Chapter One

General Introduction

1.1 INTRODUCTION

The central focus of biogeography, the analysis of the patterns of distribution of biological phenomena, has found a new audience in recent years. The search for geographical areas that contain important ecosystems and the most species has become a key issue for conservation decision-making, as the evidence of species loss and habitat modification mounts. As with most land use issues, conservation decision-making is largely a matter of real estate, and location is everything (Kiester *et al.* 1996). At least two factors influence the choice of locations for conservation. First, conservation areas have to compete with other land uses, in particular those that deliver short-term economic benefits to governments and are perceived necessary for economic development. Second, different species occupy different locations and in general, overall species diversity increases with area (Connor and McCoy 1979). Thus, finding locations that are available, species-rich, and relatively large is one of the main challenges for conservation.

Identifying locations that are appropriate for conservation is a multi-step procedure. It involves collecting geographical, biological, political, and in some cases, social data; analysing the data; and weighing potential trade-offs with other land uses. Since other land uses such as agriculture and forestry are often in competition for the same land, the decision to protect certain locations is usually done in the context of national land use planning (Williams 1997). Conservation locations that are agreed upon by governments and other stakeholders are protected in the form of national parks, nature reserves and wilderness areas (Prendergast *et al.* 1999). Collectively known as a 'protected area network', these locations are gazetted to conserve ecosystems and species in perpetuity, and in most cases exclude all other invasive land uses.

In the past, the establishment of protected area networks was usually done in an *ad hoc* manner with little regard to the distribution of ecosystems and species in a country (Pressey 1994). Emphasis was placed on areas that would protect individually threatened species, or aesthetically pleasing landscapes (Margules *et al.* 1994, Prendergast *et al.* 1999). With increasing global awareness of ecosystem degradation and species loss over the past fifteen years, attention has been given to conserving overall biological diversity. Biological diversity or "biodiversity" was adopted in the biogeography and conservation biology literature to mean the variety and variability of living organisms and the ecological complexes in which they occur (OTA 1987, Noss 1990). Simply stated, biodiversity refers to ecosystems, species and genes.

These three elements of biodiversity represent different organisational levels of the composition, structure and function of biodiversity (Noss 1990). Taken together, these three levels can be viewed as a coarse- to fine-filter of information, with ecosystem information at the 'coarse-filter' end of the spectrum and species and genetic information at the 'fine-filter' end of the spectrum (Noss 1987). Using data at the coarse end of the spectrum, as represented in a vegetation map, may provide better geographical coverage and may be more cost-effective than genetic or species data from the fine end of the spectrum. However, information on rare and restricted species and genotypes may be missed using only coarse-filter information.

In an ideal world, a protected area network would be based on the complete knowledge of the distribution of all ecosystems, species and genotypes and this knowledge would include a temporal dimension so as to deal with variation over time (Ferrier 1997). Unfortunately, a database that describes the distribution of *all* the elements of biodiversity has not yet been established for any region of the world (Ferrier 1997). This leaves no choice but to use surrogates measures of ecosystem patterns and species and genotype distributions to designate protected areas.

Determining the most appropriate surrogate measures of overall biodiversity is difficult. Measuring biodiversity at any level is proving to be harder than previously thought (Lawton *et al.* 1998, Reid 1998). Ecosystem or coarse-filter measures such as vegetation maps and environmental classifications are often the result of arbitrary classifications and are sometimes difficult to standardise, even within a region (Ferrier 1997). Species and genotypes distributions also pose a problem. With the estimates of the number of species in the world ranging from 10-100,000 million and only 1-10% of those described (Primmack 1993), the distribution of much of the world's species is poorly known (Lawton *et al.* 1994).

Because conservation decisions have to be made when opportunities arise, the use of surrogate measures of biodiversity is widely accepted in conservation decision-making, where incomplete knowledge is a reality (Ferrier 1997). What is less clearly agreed upon is which of the known surrogates of biodiversity is *best* for conservation decision-making. The most commonly used surrogates include the amount of a given environmental or ecosystem classifications in an area, number of species in an area (species richness), and in some cases, the number of genotypes in an area (Margules and Redhead 1995). Each type of surrogate has advantages and disadvantages and these have to be weighed in any conservation decision-making process. Moreover, the information available at each level of organisation may vary from country to country and region to region.

Measures of biodiversity are meaningless unless they contribute towards the achievement of a conservation goal or target. Setting explicit conservation targets has been the subject of several recent debates (see Soule and Sanjayan 1998). Whether a country adopts an overall policy of a certain amount of land (e.g. 15 %) or specific targets are set for each species and ecosystem, a conservation target must be stated before a protected area network can be designed. To track the progress towards the achievement of a stated target, methodologies are needed that are transparent and allow for the most efficient selection of protected areas with regards to the amount of land required to meet the target.

The development of such methodologies emerged in the literature in the late 1980s (Prendergast *et al.* 1999). Along with being transparent and efficient, these methodologies are systematic in nature, are data driven, and usually incorporate some flexibility in the choice of protected areas. Examples of the application of these methodologies include Rebelo and Siegfried (1990), Scott *et al.* (1993), Nicolls and Margules (1993), Margules *et al.* (1994), Pressey *et al.* (1994), Kiester *et al.* (1996), Lombard *et al.* (1997), Freitag and Van Jaarsveld (1998), Cowling *et al.* (1999).

One of the critical issues emerging from these studies is the problem of scale (Stoms 1994, Davis and Stoms 1996, Pressey and Logan 1994, Eramus *et al.* 1999, Prendergast *et al.* 1999). The geographical scale at which the elements of biodiversity are measured influences their ability to act as surrogates and this in terms may influence the location of protected areas (Flather *et al.* 1997, Reid 1998). In particular, the size of the selection unit used to examine the effectiveness of a surrogate is important and this will have a direct impact on conservation decisions. If surrogate patterns correspond at one spatial scale (e.g. regional), but decisions are made at another (e.g. local), then the resulting network of protected areas may fail to conserve the biodiversity it set out to protect. The importance of measuring biodiversity at the same scale that decisions are made is also reinforced when the network of protected areas is placed within the context of regional or national land use.

For a network of protected areas to be effective in conserving biodiversity and persist in the long-term, it must recognise threats to its existence and incorporate them in the decision-making process. Threats might include other land uses such as agriculture, forestry and mining, or encroachment of human settlements, land disputes and other socio-economic considerations. Consideration and mitigation of these threats may take on many forms and may include: multiple use zones within a protected areas network that allows for some extractive activities, impact assessments, and indices of the vulnerability of certain areas to conflicting activities.

Planning a network of protected areas is a complex task. There are no universally appropriate procedures to follow to complete this task and as with most land use planning, there may be several scenarios that achieve the same end goal (Prendergast *et al.* 1999). Several principles can be applied, however, that incorporate the 'best practices' to date. These include: (a) applying the most appropriate surrogate measures of biodiversity for a given area; (b) establishing an explicit conservation target; (c) employing a systematic selection method that is transparent and efficient; (d) using the appropriate spatial scale of analysis; and (e) incorporating an evaluation mechanisms that recognises other land uses.

This thesis explores several surrogate measures of biodiversity. Using a methodology based on the above principles, it examines how surrogate measures perform in the selection of priority biodiversity sites in Guyana, South America. Although Guyana is a country with limited biogeographical data, limited data is an inherent problem in every country. Guyana was selected because it is simultaneously under pressure to establish a network of protected areas *and* increase its economic dependency on the exploitation of natural resources (primarily forestry and mining). Thus, it provides a rare opportunity to look at conservation decision-making in the context of land use planning. The specific objectives of the thesis are outlined below.

1.2 STATEMENT OF PROBLEM, AIMS AND OBJECTIVES

1.2.1 Statement of Problem

Most countries need to make conservation planning decisions but have limited data on which to base the decisions. This thesis examines the problem of designating optimal sites for biodiversity protection using the data available for Guyana. In particular, the thesis looks at different surrogate measures of biodiversity, assumptions associated with these surrogates, and the role of spatial scale and external threats to biodiversity in designating sites for a protected area network.

1.2.2 Aim and Objectives

The aim of this thesis is to provide guidelines for the effective use of available data in the development of efficient, flexible, and practical biodiversity conservation initiatives in Guyana. The objectives of this thesis are to:

a) Assess and compare the influence of different surrogate measures of biodiversity on the selection of priority biodiversity sites in Guyana.

b) Provide the first comprehensive models of terrain and climate for Guyana and use these models to derive environmental classifications (domains) to be use as a surrogate measure of biodiversity and as selection criteria for priority biodiversity sites.

c) Contribute to the debate on patterns of species distribution and cross-taxon congruency and its usefulness and applicability to conservation decision-making by describing the patterns of distribution of priority biodiversity sites using species richness, irreplaceability and the 'surrogacy effectiveness' of ten different taxonomic groups.

d) Contribute to hierarchy and scaling theory by examining how observed patterns of species distributions translate from one level of scale to another level.

f) Compare the different outcomes for priority sites when indices of vulnerability are used to quantify external threats to biodiversity.

g) Present a protocol for establishing a protected area network in Guyana

Chapter two of this thesis describes the biophysical and socio-economic setting of Guyana. Guyana is a poor country that faces the challenge of establishing and managing its first protected area network with limited resources and pressure to exploit its natural resources to increase economic growth. The chapter attempts to demonstrate that despite economic hardship and pressure to increase natural resource use, Guyana is biologically very rich, contains unique flora and fauna, and still has vast tracts of near pristine forests and savannas that warrant conservation.

Chapter three is a review of the relevant literature on the factors influencing patterns of biodiversity distribution, measurements of biodiversity, methods for selecting protected areas, issues regarding the spatial of analysis and choice of area with regard to other land uses. The chapter also presents a conceptual framework for conservation decision-making that incorporates some of the necessary criteria, targets, methods and evaluation processes for conservation decision-making.

Chapter four uses primary data on climate and terrain to generate climate surfaces and a digital elevation model of Guyana. These surfaces are then used in conjunction with maps of the lithology and soil fertility of Guyana to generate classification of environmental domains. Environmental domains are in turn used as a surrogate measure of biodiversity. Different classifications and different conservation targets are used to compare the location of priority biodiversity sites. The locations of priority sites are compared with sites selected using vegetation classes.

Chapter five examines the patterns of species distribution in Guyana and investigates different species-based surrogates of biodiversity. First, species richness and the restricted range values of species are compared. Second, recorded and modelled species locational data are used to select priority biodiversity sites using two different criteria: species richness and irreplaceability, a measure of uniqueness. Thirdly, sites selected using richness and irreplaceability are compared for several taxonomic groups. Lastly, sets of sites selected using richness and irreplaceability are compared with those selecting using environmental domains and vegetation classes.

Chapter six uses the data presented in chapter five to examine the influence of selection unit size on: a) the spatial patterns of species richness; b) the efficiency of representing known species using different selection unit sizes; c) the overlap in the location of priority biodiversity sites from one selection unit level to another; and d) the influence selection unit size has on the ability of certain taxonomic groups to act as surrogates for one another.

Chapter seven attempts to incorporate an index of vulnerability, along with an index of biodiversity priority into the selection of priority conservation sites. The vulnerability index used is an index of how threatened certain areas are with regard to specific anthropomorphic activities - agriculture and forestry. Chapter seven also presents a protocol on how biodiversity conservation decisions could be made in Guyana to maximise the retention and long-term persistence of biodiversity.

Chapter eight summarises the main findings of the thesis and its contribution to conservation-decision making.

There are many issues relating to the location of protected areas that need attention and some of these are addressed in this thesis including different surrogate measures of biodiversity, spatial scales and perceived threats. The thesis does not attempt to examine the best size, shape or configuration of a protected area network for Guyana. The other issues pertaining to protected area design, in particular shape, and adjacency are very important issues; however, they are the subjects of theses themselves. Furthermore, the thesis only examines terrestrial species. This is primarily due to the lack of data for freshwater and marine organisms. Lastly, it is hoped that the results of this thesis are taken into consideration when the Government of Guyana decides on the location of its protected areas. However, this thesis is not a report on where definitive areas should be located in Guyana, but rather a theoretical examination of the factors that may influence the location of protected areas.

Chapter Two

Guyana: The Case Study

2.1 NATIONAL CONTEXT

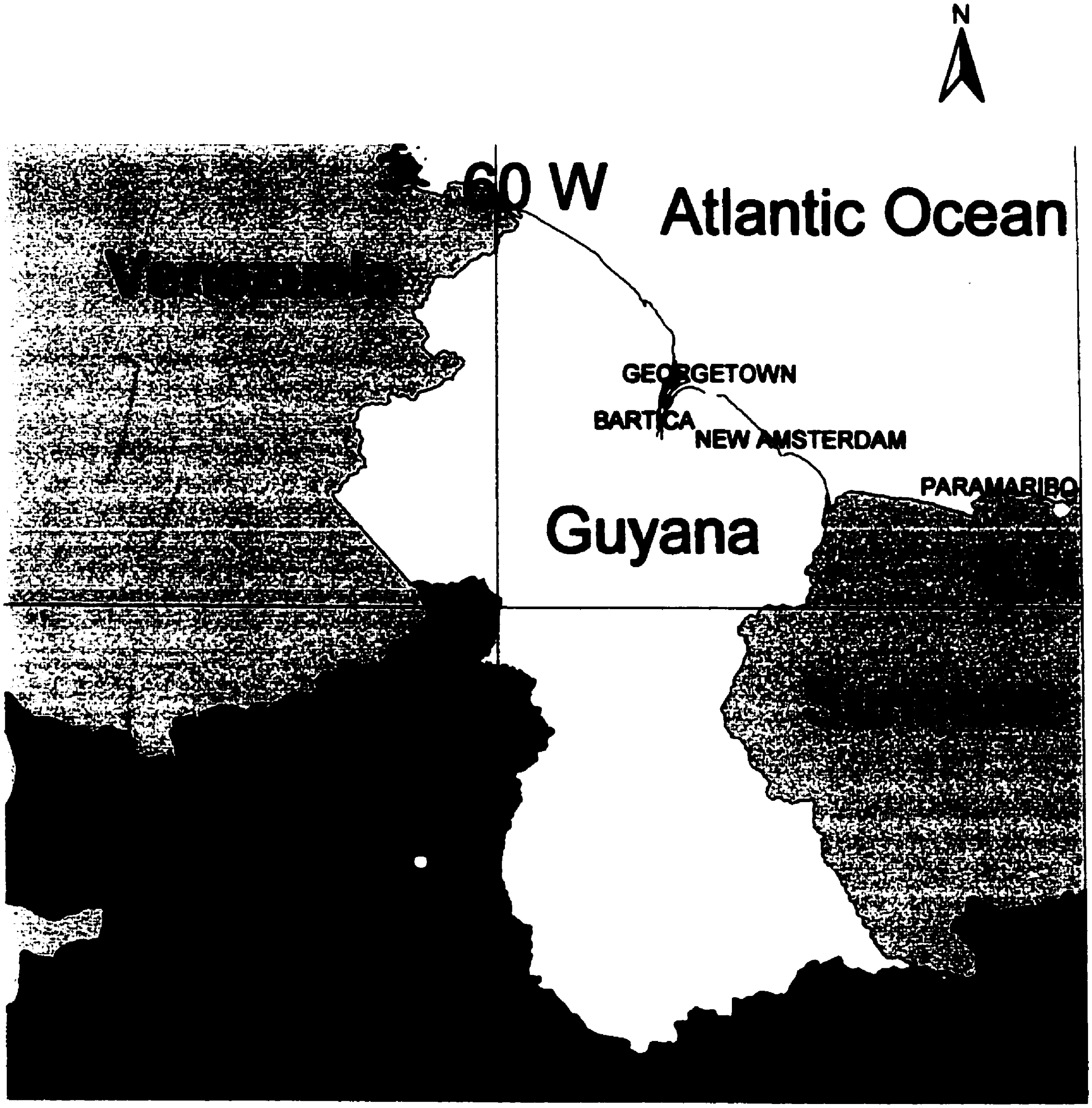
2.1.1 Geographical Situation

The Co-operative Republic of Guyana is one of eight countries that occupy the vast Amazon River Basin (Figure 1). The name 'Guyana', is an Amerindian name that means land of many waters and reflects the complex river systems of Guyana. Located on the north-eastern edge of South America between latitudes 1° 10'55"N - 8° 33'22"N, and longitudes 56° 28'27"W - 61°23'24" W, Guyana lies over part of the Guiana shield, a very rich biogeographic region. To the north, it borders the Atlantic Ocean for some 430 km, to the east, the Republic of Suriname, to the west and north-west, the Republic of Venezuela and to the south and south-west, the Federative Republic of Brazil. The country covers 214,970 km^2 (approximately 21.5 million hectares) and is dominated by forests, which cover over 75 % of the country.

2.1.2 Demography

The population of Guyana was 723,827 at the last census of 1991 (Government of Guyana 1991). Although the average national density is approximately 3.4 person/km^2, almost 90 % of the population live in towns and villages along the coastal belt that occupies only 10 % of the territory, thus greatly increasing the density along the narrow coastal strip. In the interior or hinterland of Guyana, the population density is as low as 0.56 person/km^2. There is one city in Guyana, the capital, Georgetown (population 151,000), and four towns: Linden (pop. 35,000), New Amsterdam (pop. 25,000), Corriverton (pop. 13,700) and Bartica (pop. 6,300). Together, these towns account for approximately 30 % of the Guyanese population. The ethnic composition of Guyana is roughly 49% East Indians,

Figure 1: Location of Guyana



Source; Conservation International 1996

200 kilometers

35.5% Africans, 8 % European, 6.8 % Amerindian, 0.3 % Chinese and 0.4 % other groups (Government of Guyana 1991). The approximately 41,000 Amerindians, from 11 distinct tribes, live in the interior of the country and have title to approximately 1.39 million ha. of land, which is divided into 65 reservations established under the Amerindian Act of 1976.

For administrative purposes, Guyana is divided into ten regions (Figure 2). Each region is governed by a local administration called a Regional Democratic Council that has jurisdiction over regional matters. The population and size of each region varies greatly, with the largest regions (regions 7,8 and 9) having the lowest populations (Table 1, Figure 2).

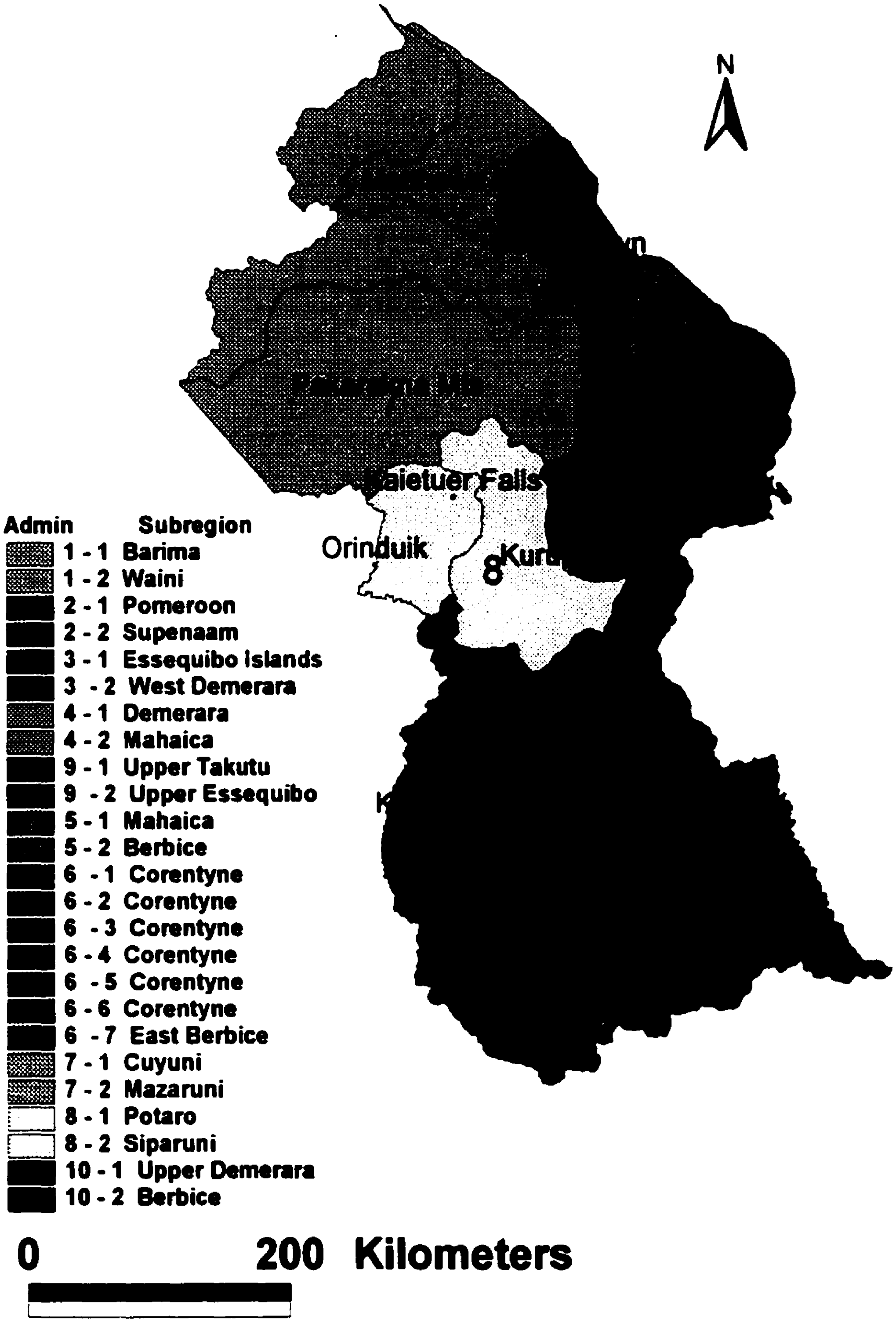
Table 1: The Administrative Regions of Guyana

Region	**Name**	**Area (km^2)**	**Population**
Region 1	Barima-Waini	18943.8	18,600
Region 2	Pomeroon-Supenaam	5495.718	42,800
Region 3	Essequibo Islands-West Demerara	3883.531	91,350
Region 4	Demerara-Mahaica	2030.794	297,000
Region 5	Mahaica-Berbice	3818.913	49,500
Region 6	East Berbice Corentyne	43720.03	142,800
Region 7	Cuyuni-Mazaruni	47996.05	15,300
Region 8	Potaro-Siparuni	21024.32	5,700
Region 9	Upper Takutu-Upper Essequibo	54814.68	15,000
Region 10	Upper Demerara-Berbice	9833.655	39,000

2.1.3 The Economy

Guyana is regarded as one of the poorest countries in the Western Hemisphere. During the 1970s and 1980s, Guyana declared itself a Co-operative Socialist Republic and nationalised most of its private enterprises (Williams 1997). The expansion of the public sector into almost all areas of the economy was exacerbated by weak public sector management and poor international markets for Guyana main export items, bauxite and sugar. During these years Guyana suffered

Figure 2: Administrative Regions of Guyana



Source: Centre for the Study of Biological Diversity 1996 extreme economic hardships (Government of Guyana 1994). By 1988, Guyana embarked on a reorientation of economic policy in line with a structural adjustment policy from the International Monetary Fund to curb the downward spiral of the economy. In the twelve years of a socialist regime, Guyana's GDP dropped 32 %. In 1992, a new government was elected and it set out to rebuild the economy. The estimated Gross National Product (GNP) per capita of $US350 in 1993 rose to $US770 per capita in 1998 with growth during those years estimated at 7.0 % (Government of Guyana 1995, World Bank 1998). However, the extreme poverty of the country and burden of foreign debt has placed an enormous pressure on the Government to diversify its economy. The major sectors of Guyana's economy are agriculture, fisheries, mining, and forestry (Government of Guyana 1994).

2.1.3.1 Agriculture and Fisheries

Agriculture accounts for about 30 % of Guyana's GDP, with most of the land devoted to rice and sugar cultivation which are the two main agricultural exports. Fish and shrimp also play an important role in Guyana, as they are the main source of animal protein and also account for a significant percent of Guyana's agricultural exports (Government of Guyana 1994).

2.1.3.2 Mining

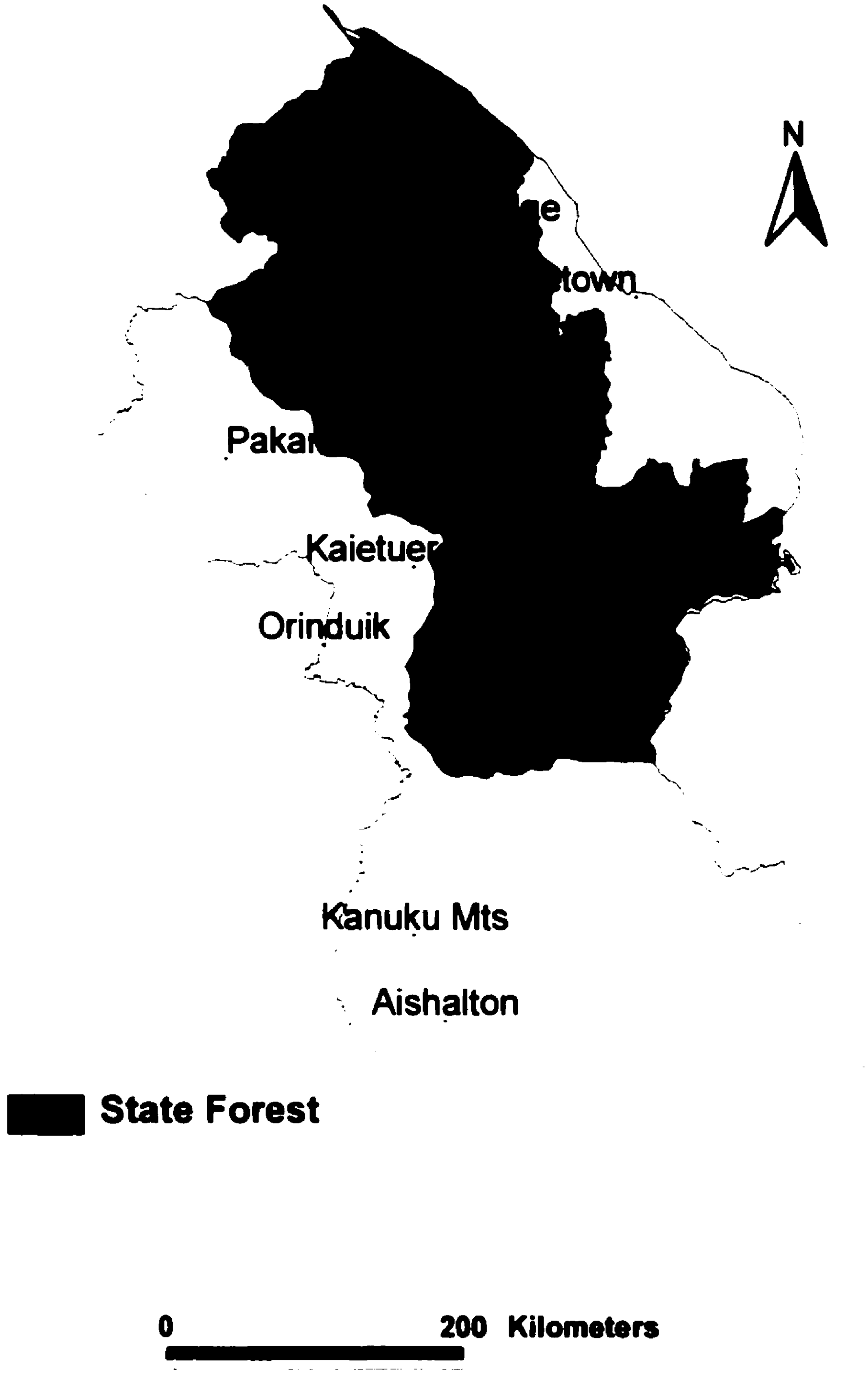
Mining accounts for over 10 % of the GDP and the sector is primarily based on mining bauxite, gold and diamonds. Guyana is one of two producers of premium calcined bauxite, however the weak international market for bauxite has limited Guyana's export. Due to the unique geology of the Guiana Shield, Guyana has recently expanded its gold and diamond mines to include one large-scale gold mine, Omai, and many medium- and small-scale operations. Gold is now the major mineral export and gold mining is rapidly expanding. Fluvial gold and diamond mining activities are already causing widespread environmental damage to inland rivers and the Amerindian communities dependent upon riverine resources (Government of Guyana 1994). The proliferation of gold and diamond mining has also been associated with pollution in the rivers from the chemicals (mostly mercury and cyanide) used to extract the minerals. There is very little regulation of mining activities due to the remoteness of most mining activities, poor infrastructure, and a weak regulatory body. Improved monitoring capacity of mining activities is a goal of the current government and an Environmental Protection Agency has been established to oversee the industry's compliance with new environmental laws (World Bank 1998). Although dredging and chemicals are impacting Guyana's waterways more and more, the impact is difficult to quantify, as the relative isolation of activities has kept them from most scrutiny.

2.1.3.3 Forestry

Guyana has approximately 16.3. million ha. of rain or seasonal forest and another 1.7 million ha. of dry evergreen forest that co-exist with savanna on sandy soil (Sizer 1996, Amsterdam 1997). Of the 16.3 million ha., 9.1 million ha. are currently State Forests under the management of the Guyana Forestry Commission (Figure 3). The remaining forests are under the control of the Department of Lands and Survey. The boundaries of the State Forest are currently under revision and are expected to include a further 4.5 million ha.(Ter Steege 1998).

By 1994, less than 1 % of the country had been deforested (Government of Guyana 1994). While Guyana has practiced relatively sustainable selective logging for decades, the pressure on the Government to increase its economic growth by expanded its forestry sector has seen a dramatic increase in the deforestation rates (Amsterdam 1997). The annual timber harvest is approximately 240,000 m^3 and revenue from this presently accounts for 2-3 % of Guyana's GDP (Government of Guyana 1994, Amsterdam 1997). Timber is Guyana's most important forest product and greenheart (*Chlorocardium rodiei*) and purpleheart (*Peltogyne* spp.) are the best known, and most intensely harvested species for export (Government of Guyana 1994). Until the 1990s, greenheart accounted for 40-50 % of the total volume of timber harvested and has been

Figure 3: State Forest in Guyana



Source: Guyana Forestry Commission;
Centre for the Study of Biological Diversity 1996

severely overharvested (Government of Guyana 1994, Sizer 1996). In 1991, a Malaysian/Guyanese consortium was granted a timber concession of approximately 1.6 million ha. in the north-west of Guyana. Barama Company Limited established an integrated logging and plywood production based on the harvest of 12 plywood species. By 1994, plywood from Barama overtook greenheart as the primary export timber product and accounted for 68 % of the wood product exports from Guyana (Sizer 1996). As the need for more growth in the economy increases, the Government is under pressure to consider more large timber concessions, particularly in the south of the country where timber harvesting has been almost absent and access difficult.

2.1.3.4 Wildlife Trade

Guyana has a relatively large trade in wildlife. Wildlife trade accounted for approximately 1 % of the country's GDP in 1995. In 1988, Guyana was ranked tenth in the world in the number of birds officially exported (Government of Guyana 1994). Birds (mostly parrots) account for 20 % of the animals exported, but brought in 75 % of export revenue. The remaining 80 % of animals traded were primarily reptiles (Government of Guyana 1995). Although Guyana is a signatory to the Convention on International Trade in Endangered Species (CITES), it is estimated that the illegal trade of wildlife is prolific due to the inadequate funding, ill-equipped and understaffed Wildlife Services Division which oversees export licences (Government of Guyana 1994). Along with CITES, Guyana is signatory to and ratified the Convention on Biological Diversity in August 1994. The Government's has also pledged its commitment to environmental protection and natural resource conservation in its National Environmental Action Plan (NEAP) completed in 1994.

In the NEAP (Government of Guyana 1994) the Government affirmed its commitment to the principal of sustainable development and stated that it will "conserve and use the environment and natural resources of Guyana for the benefit of both present and future generations" (Government of Guyana 1994). To this end, the Government pledged to create a national system of protected areas to conserve its biodiversity.

2.2 BIOPHYSICAL PARAMETERS

2.2.1 Climate

The climate of Guyana is tropical, being largely determined by movements of the Intertropical Convergence Zone (Ramdasss and Haniff 1990). With its close proximity to the Equator, the primary determinant of changes in temperature is altitude (Hydrometeorological Service 1992). Most parts of Guyana are characterised by two dry seasons (mid-January to mid April and mid August to mid-November) and two wet seasons a year (Hydrometeorological Service 1992, Boggan *et al.* 1997). One exception is the southern Rupununi savannas, where a dry season of seven months and a wet season of five months is common (University of Utrecht 1995).

2.2.2 Topography

The elevation in Guyana ranges from just below sea level in some parts of Georgetown to 2198m at the highest part of Mt. Roraima that lies within the border of Guyana (Mt. Roraima reaches 2,772m at its peak in Venezuela). The highest peaks in Guyana are found in the Pakaraima Mountains and include Mt. Wokumung (2,134m) and Mt. Ayanganna (2,042m). Guyana is characterised by its central low lying forests bordered by the Pakaraima Mountains to the west and its relatively low lying savannas interspersed to the south-west by the Kanuku Mountains.

Topographically, the country can be divided into four regions: a) the low coastal plains; b) the sandy rolling lands; c) the highland/Pakaraima region; and d) the Pre-Cambrian lowlands (Ramdasss and Haniff 1990).

2.2.2.1 The Low Coastal Plains

The low coastal plains lie partially below sea level and consist of a narrow strip along the coastline. The plain covers 7.5 % of Guyana and is a result of the meeting of two formations, the Coropina Formation (1 million years old) and the Demerara Formation (0.01 million years old) (Ramdasss and Haniff 1990). This narrow strip is the only agriculturally fertile area of Guyana and is inhabited by 90 % of the population (Ramdasss and Haniff 1990, GAHEF 1992).

2.2.2.2 The Sandy Rolling Lands

The sandy rolling lands lie to the south of the low coastal plain and cover approximately 12 % of the country. They are characterised by wallaba forests on white sands. The sandy rolling lands are approximately 11 million years old and are economically significant because bauxite deposits occur below the white sand. The region is also important as a water catchment area for the low coastal plains (Ramdasss and Haniff 1990).

2.2.2.3 The Highland/Pakaraima Region

The Highland/Pakaraima region lies in the mid-western part of the country. It occupies approximately 14 % of the country and is dominated by massive Pre-Cambrian crystalline rocks of the Guiana Shield (Ramdasss and Haniff 1990). The underlying Roraima Formation extends into Venezuela and Brazil with Mt. Roraima at the meeting point of the three countries. The region is known for its gold and diamonds deposits. The soils favour the growth of tropical rain forests at lower elevations.

2.2.2.4 The Pre-Cambrian Lowland

The Pre-Cambrian lowland covers the remainder of the country (66.5%) and is the largest region. This region is primarily low, undulating land between 90-120 m with a few peaks over 900 m in the south (Kanuku Mountains) (Ramdasss and Haniff 1990). It is dominated by tropical rain forests and savannas in the south-eastern and south-western part of Guyana.

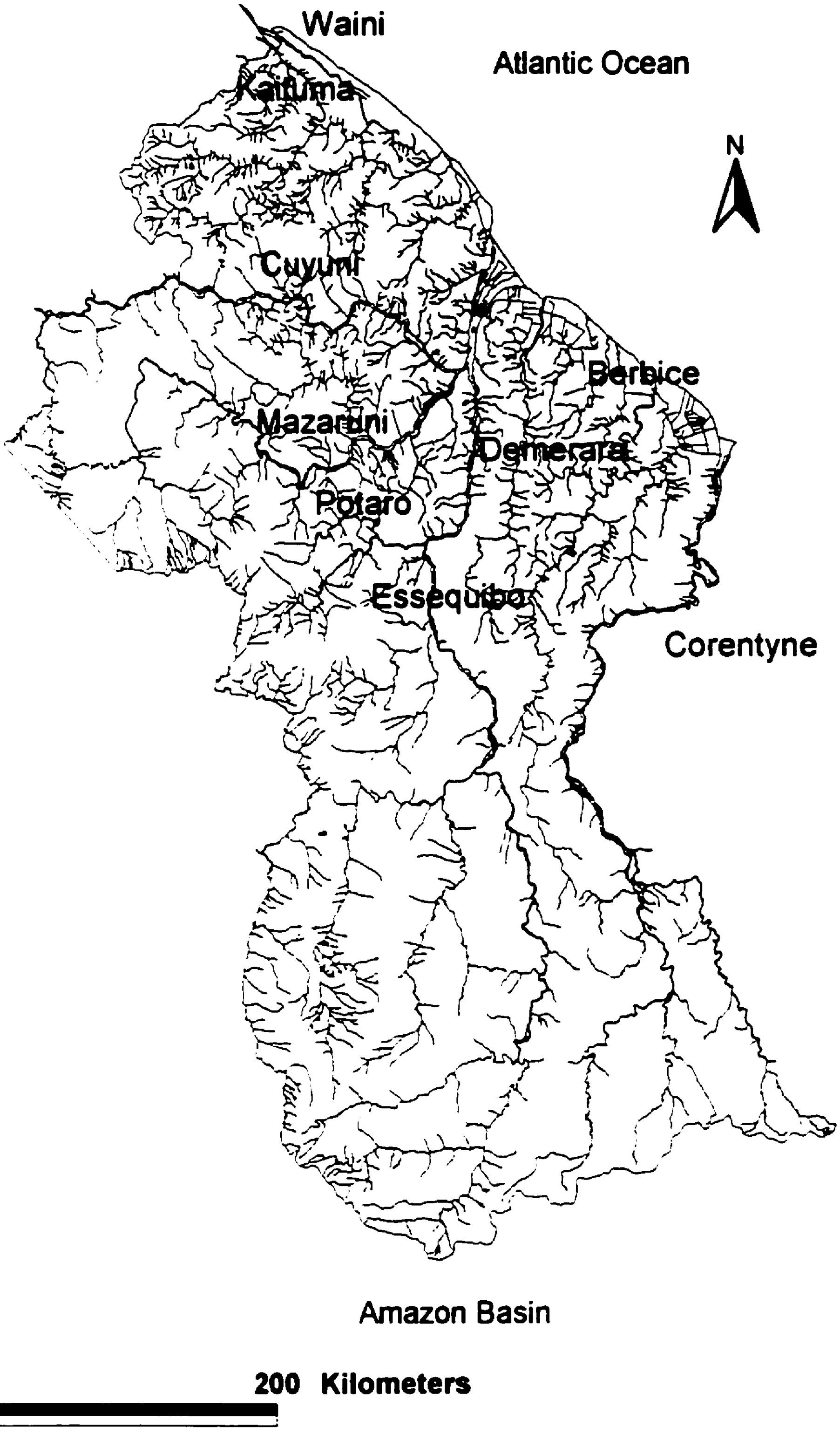
2.2.3 Hydrology

Guyana has several large rivers (Figure 4) and these include the Essequibo, Demerara, Cuyuni, Berbice, Mazaruni, Potaro and Courentyne rivers. The country has eight main river basins that drain both into the Atlantic Ocean to the north and the Amazon basin to the south (Figure 4), although most rivers flow northwards (Ramdasss and Haniff 1990). Guyana is covered in streams and tributaries that, along with the rivers, act as the main passageways for travel into the interior of the country (Figure 4).

2.2.4 Geology and Soil

Underlying most of Guyana is the Guiana shield, which covers a large area from the Atlantic Ocean to the Orinoco and Amazon rivers. The Guiana shield is an old Pre-Cambian land mass, made up of metamorphosed and folded formations of sedimentary and igneous origin, estimated to be between 4 billion – 590 million years old (McConnell and Choubert 1975). Overlying the central portion of the Shield are the Roraima sediments that, although lacking in fossils, are believed to have been laid down on the Guiana Shield during the Cretaceous Period (140 to 68 million years ago) probably as shallow marine or brackish water deposits. The Roraima formation consists of pink, yellow, and white sandstones, red quartzites, green, black, and red shales, conglomerates, and boulder beds. Erosion has decreased the size of the formation, and the remaining sediments extend west from the Kaieteur escarpment in central Guyana, forming the Pakaraima Mountains, and on through parts of Venezuela, Colombia, and south into Brazil. Within this area, erosion has created vertical flat-topped peaks called "tepui." These table-like formations are virtually inaccessible and, due to their unique flora and fauna, are often referred to as "The Lost World."

Figure 4: Rivers and Streams of Guyana



Source: Centre for the Study of
Biological Diversity 1996

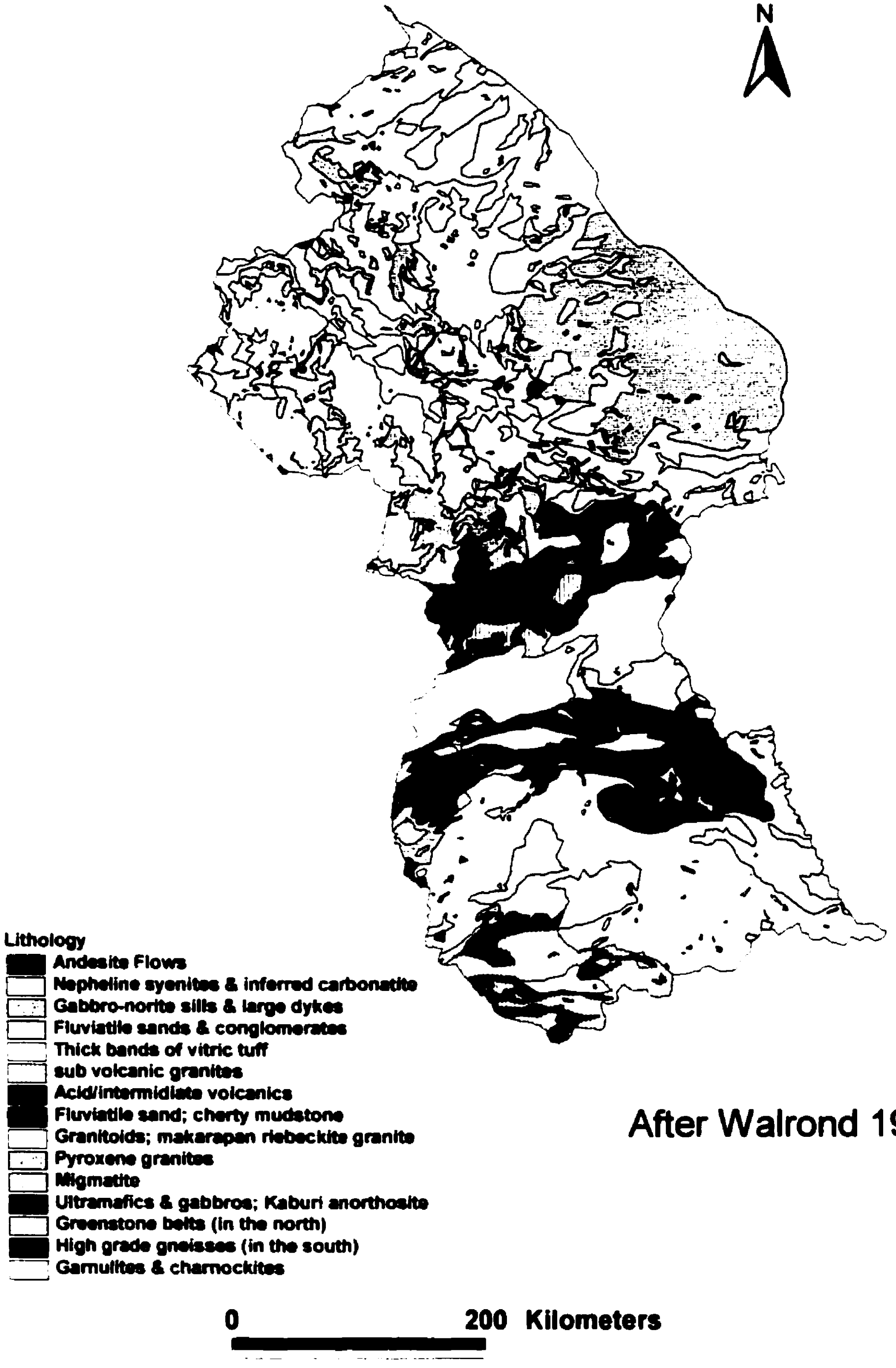
There are 14 types of parent material or lithology in Guyana (Figure 5). Migmatite, granitoids and high grade gneisses are the predominant types across Guyana (Walrond 1987). The varied geology of Guyana has given rises to 8 main soil types (UNDP 1964), including vast areas of white and brown sands. Most of the good agricultural soils lie on the Low Coastal Plain. These soils consist primarily of clays and organic soils. The central forests of Guyana grow on a mixture of white sands, podzols (loamy) and brown sands. The most fertile area are found along the eastern coast, in the north-central part of the country, and in the south-eastern corner and correspond to the podzol (loamy) soils and the brown sand areas (UNDP 1964).

2.3 BIOGEOGRAPHY

2.3.1 Biogeographical Provinces and Communities

Udvardy's (1975) classification of biogeographical provinces at a global scale placed Guyana within the Guyanan (tropical humid forest) and Campos Limpos (tropical grasslands and savannas) adjacent to the Amazonian biogeographical provinces. Olson and Dinerstein's (1998) biogeographical realms puts Guyana in the "Guyanan forests" realm along with Suriname and French Guiana and disregards the distinct Amazonian characteristics of the southern half of Guyana (including the savannas). At a more local scale, several classifications of Guyana's biogeographical provinces and ecosystems have been undertaken. They include: Fanshawe (1952,1954), Harrison (1958), Eden (1964), Hills (1965, 1969), Sampson and Bell (1972). These studies generally agree that there are three biogeographical provinces in Guyana: a) the coastal biogeographical province; b) the savanna biogeographical province; and c) the forest biogeographical province. These provinces encompass twelve biotic communities (Ramdasss and Haniff 1990) (Table 2).

Figure 5: Lithology of Guyana



After Walrond 1987

Table 2: Biogeographical provinces and biotic communities of Guyana (after Ramdasss and Haniff 1990)

Province	**Biotic Community**	**Features**
Coastal	Coastline community	Saline mudflats, mangrove forests, sand and shell beaches. Largest concentration found on the north-western shoreline, west of the Essequibo river. This community hosts many spawning fish and invertebrates.
	Estuarine community	Tidal mudflats along the estuaries of the main rivers. Subject to periodic or continuous flooding.
	Riverine community	Wetlands at the mouth of the rivers characterised by regular flooding. Dominated by ferns, palms, mora and crabwood.
	Palustrine community	Marshes and swamps in the river floodplains, as well as "water savannas".
	Lacustrine community	Natural lakes and water reservoirs found mainly along the coast. Lakes generally have a low pH and low concentrations of oxygen.
Savanna	Intermediate or Berbice savanna	Found on the Sandy Rolling land near the coast. These savannas are drained by several rivers, including the Ituni and Ebini and are characterised by bunch grass with scattered patches of small trees.
	Rupununi savanna	These savannas are an extension of the Rio Branco savannas of Brazil and are found on the Pre-Cambrian Lowland region. These savannas are drained by the Rupununi river and tributaries of the Essequibo river. Both dry savannas (xerophytic) and wet savanna vegetation is found, predominantly grasses, bunchgrasses, and sedges, with significant differences in the floristic of the northern and southern savannas.
Forest	Tropical moist forest	This is the most widespread forest type in Guyana and it covers approximately half the country at elevations below 300m. The main tree species include greenheart, purpleheart, morabukea and

		kakaralli.
	White sand forest	These forest are considered to be the orginial vegetation of Guyana and the climax vegetation. These forests are typically dry evergreen forests and are dominated by wallaba, ituru and muri.
	Brown sand forest	Brown sand forests occur on the borders of white sand forests on well-drained brown sand. The dominant species include greenheart and morabukea as well as shrubs, liana and epiphytes.
	Swamp forest	Swamp forests are found in the poor drained coastal areas in the north-west of Guyana. Tree diversity is very low in these forest and the dominate species include mora, corkwood and crabwood.
	Montane Forest	Montane forests are divided into lower montane forests that flourish on the lower mountain slopes of the Pakaraima, Kanuku and Akarai mountains at elevations below 365 m, and high montane forests that occur up to 1535 m. At elevations above 1535 m, elfin forests occur. Higher elevation vegetation includes mosses, epiphytes, ferns and dwarf palm trees.

2.3.2 Vegetation Map

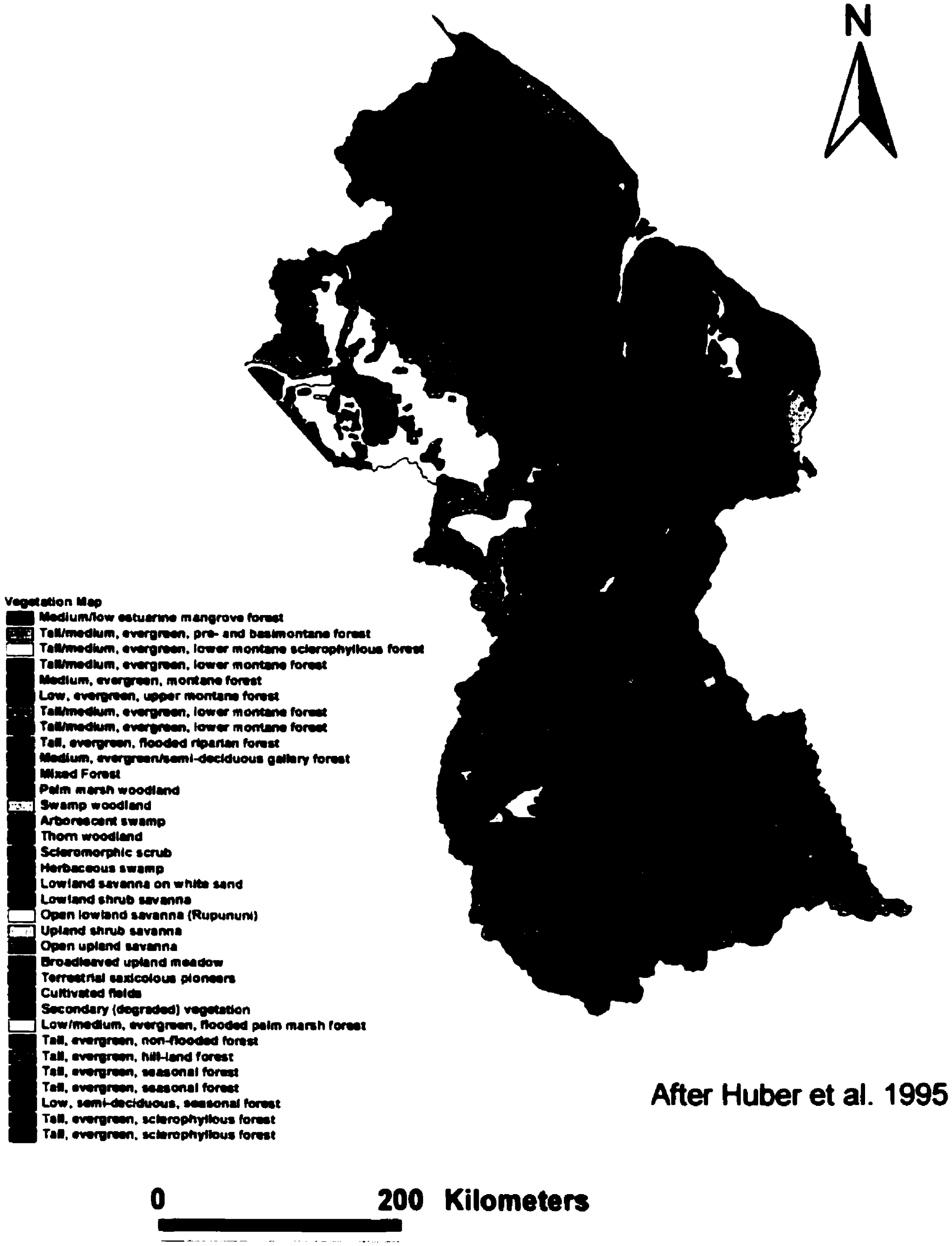
The vegetation of Guyana is determined primarily by the underlying geology, altitude, and annual amount of rainfall. The most recent vegetation map of Guyana, produced by the Smithsonian Institution's Biological Diversity of the Guianas Program, was based on LANDSAT TM images taken between 1990-1995 (Huber *et al.* 1995) (Figure 6). This map shows 34 major division of vegetation types, based on differentiation from the satellite images and from botanical surveys (Huber *et al.* 1995). The classifications of the vegetation types are based on Fanshawe's (1952) original classifications with several additions. There are, however, several areas of the country, such as the south-east corner of the country, where no surveys have been conducted (due to a border dispute with

Surinam) and the vegetation type is poorly defined. This area contains dense forest, but little is known about the dominant tree species. A recent study by Ter Steege (1998) using FAO forestry survey data from 1966 to 1973, showed five clusters of forest regions in Guyana based on dominant tree species. These five regions: the southern wet forests, the southern dry forests, the Pakaraima wet forests, the central Guyana wet forest and the north-west Guyana wet forest, are distinguishable based on forest composition and diversity (Ter Steege 1998). To date, the vegetation map of Huber *et al.* (1995) provides the most comprehensive information on the location of vegetation communities in Guyana and can be considered a baseline map for describing the flora of Guyana.

2.3.3 Flora

Guyana is one of the richest countries in terms of its flora and fauna. It is estimated that over 8000 plant species occur in Guyana and of these, over 6,500 vascular plants have already been documented (Boggan *et al.* 1997). The flora of Guyana has been studied by the Biological Diversity of the Guianas Program (BDG) of the Department of Botany, National Museum of Natural History, Smithsonian Institution, which has been operating since 1983. In conjunction with the Royal Botanic Garden at Kew, England; the British Museum of Natural History, England; the University of Utrecht Herbarium, the Netherlands; the Royal Ontario Museum, Canada; the University of Guyana, Guyana, and the American Museum of Natural History, USA, the Smithsonian has databased over 25,000 records. The known flora of Guyana includes vascular plants (such as flowering plants, gnetophytes, cycads, conifers, and ferns) and bryophytes (such as mosses, hornworts, and liverworts) (Boggan *et al.* 1997). Of these, only about 3% are introduced and naturalised. The families with the largest number of species in Guyana are the Leguminosae (530 species) and the Orchidaceae (500 species). Other large families are the Rubiaceae and the Poaceae. It is estimated that half of the plant species found in Guyana are endemic to the greater Guiana shield area

Figure 6: Vegetation Map of Guyana



After Huber et al. 1995

that covers the Guianas as well as parts of Brazil and Venezuela. The number of species endemic only to Guyana is difficult to estimate.

Although collecting expeditions have been on-going for several decades, the inaccessibility of certain areas in Guyana (in particular the south-east corner) have left many gaps in the data. The restriction to certain areas is mostly political rather than logistical, and data from these areas will always to be difficult to acquire. In addition, like most collections world-wide, there is a noticeable concentration of collecting sites along accessible roadsides and near airstrips.

2.3.4 Fauna

The information on Guyana's fauna is poor in comparison with data on plants. There are nearly 1,200 known vertebrate species of which 728 are birds, 198 mammals, 137 reptiles and 105 amphibians (Ramdass and Haniff 1990, Government of Guyana 1994). Little information is available for fish and invertebrates other than butterflies and termites. A database of known species localities has been compiled by the BDG, however it is heavily biased towards birds and mammals (Funk, pers. com.).

2.3.5 Status of Flora and Fauna

2.3.5.1 Status of plants

To date, there are no plants listed as endangered, threatened or vulnerable in Guyana. There are, however, several species of commercially sought-after tree species in serious decline and these include: greenheart (*Chlorocardium rodiei*), morabukea (*Mora gonggrijpii)*, bulletwood (*Manilkara bidentata*), mora (*Mora excelsa*), crabwood (*Carpa guianensis*) and wallaba (*Eperua* sp.) (GAHEF 1992).

2.3.5.2 Status of Animals

Due to the limited accessibility of most of Guyana's hinterland, most animal species have enjoyed relatively low hunting pressures; however, this is rapidly changing with the gradual expansion of resource exploitation in the hinterlands. Several species known to be rare or threatened throughout most of their range are relative common in Guyana. There are 144 species of animals listed by CITES as at risk of endangerment in Guyana. This is mostly due to the over harvesting and trading of certain species as mentioned in section 2.1.3.4. Of the 144 species at risk, 43 are listed as endangered or threatened in Guyana. These are mostly bird, mammal and reptile species and include the Harpy eagle (*Harpia harpyja*), the roseate spoonbill (*Ajaja ajaja*), the tapir (*Tapirus terreatris*), (Ramdasss and Hannif 1990). The four marine turtles occurring in Guyana (the green turtle, leatherback turtle, hawksbill turtle, and Pacific Ridley), are also heavily hunted and their eggs are collected.

2.4 CONSERVATION ACTIONS

2.4.1 Protected Areas

Discussions on the need to establish a protected area network in Guyana date as far back as the 1950s. At present, there is only one gazetted national park, Kaieteur Falls National Park, which covers approximately 300 ha. The Government has recently put before Parliament a proposal to extend the limits of the park to cover an area of 580 km^2. In addition, under the recently passed Iwokrama Act (March 1996), half of the 360,000 ha. of the Iwokrama Rain Forest site is to be set aside as a Wilderness Preserve. A number of studies and consultancy reports exist on the need, rationale, criteria for selection, and steps needed to establish a protected area network in Guyana (e.g. Dalfelt 1978, Ramdasss and Haniff 1990, GAHEF 1992, Agriconsulting 1993, Conservation International 1993). Some of these documents identify a set of recommended protected areas at the country level or at a regional (Amazon Basin) level, and some identify the need to protect specific areas, such as Kaieteur Falls and the Kanuku Mountains. Most of these reports also provide suggestions on management categories and sites of international importance. However, few use ecosystem or biogeographic classifications of Guyana and none of these reports use comprehensive species data. The exception to this is Ter Steege (1998) who used data from forest inventories dating from 1966 to 1973 carried out by FAO to classify forest types in Guyana. Ter Steege (1998) used the forest classifications in turn to determine priority areas for establishing protected areas in Guyana. The five forest regions derived by Ter Steege (1998), corresponded well with already derived forest vegetation types. The suggested protected areas included areas already suggested by previous studies (Ramdasss and Haniff 1990, Agriconsulting 1993, and Conservation International 1993), however because the study used only forestry data, the suggested areas for protection excluded the savanna regions.

2.4.1.1 Kaieteur Falls National Park

Kaieteur Falls is a dramatic waterfall that cascades down of 226 metres of vertical rock. Located along the Potaro River at 5°10' N latitude and 59°29' W longitude, Kaieteur Falls National Park is the only national park in Guyana. Established in 1929 by the British Commonwealth, Kaieteur Falls National Park originally encompassed 11,400 ha. In 1973, the park's boundaries were reduced to 300 ha., (the area immediately surrounding the falls) to take advantage of the mineral resources of the area. In 1993, the Government of Guyana drafted legislation to expand the park to 580 km^2 and is in the process of drafting a comprehensive plan to manage the area for ecotourism (Government of Guyana 1998).

The waterfall is one of the most dramatic places in Guyana and it is the number one tourist attraction of the interior. In addition to its outstanding geophysical features, the Potaro Plateau, which includes Kaieteur Falls, supports many different habitats. The mist from the falls has created a cloud forest habitat at the top of the falls along the riparian forest that supports more epiphytes than a typical rain forest (Kelloff 1999). There are several endemic species of plants found in the Kaieteur area and a checklist of plants has been compiled by Kelloff and Funk (1999). Little is know about the animal species around Kaieteur Falls. Preliminary studies have indicated that this area is particularly rich in animal life and historically, agouti, paca, tapir, red brocket, deer, collared peccary, bushmaster, labaria, jaguarundi, and golden frogs were recorded around the falls (Kelloff 1999).

2.4.1.2 Iwokrama Rainforest Project

The Iwokrama Rainforest project site is located in central Guyana, 300 km south of Georgetown. The project site is part of a program funded by the Government of Guyana, the Global Environment Facility and the Commonwealth Secretariat to establish a centre of excellence for forest research that would serve the global scientific community. The Government of Guyana contributed an area of 360,000 ha. of tropical forest within the vicinity of the Iwokrama mountains to establish a research site. The area is covered in lush, lowland tropical forest and is characterised by tall tropical trees with dense canopy 20-30 metres high and is demarcated by the Essequibo, Siparuni, Takatu, and Sipariparu rivers.

In March 1996, the Government of Guyana enacted the Iwokrama International Centre for Rain Forest Conservation and Development Act. Under this legislation, approximately half of the Centre's 360,000ha. site will eventually be managed as a wilderness preserve while the remainder will be used for the sustainable utilisation of natural resources. Detailed flora and fauna surveys have been undertaken over the last two-three years and surveys have recorded 2,000 vascular plant species, 450 species of birds, 206 species of fish, 120 species of snakes, lizards and frogs and 105 species of mammals (Iwokrama 1999). Importantly the forest has healthy populations of top predators such as Harpy eagles, pumas, jaguars and black caiman and other lowland rainforest species that are becoming increasingly rare in other neotropical countries because of human impacts.

2.4.2 Proposed Conservation Actions

Aside from Kaieteur Falls National Park and the Iwokrama Rainforest project, Guyana does not have any other protected areas or an agreed upon plan of where future protected areas should be located. The Government of Guyana has made a firm commitment to establish a network of protected areas in the very near future (Government of Guyana 1994, Government of Guyana 1998). According to the Government, "the goal of protected area network would be to conserve globally important biodiversity through the viable representation of each ecosystem in a national protected area network. The system would encompass sites representative of all the country's major ecosystems and contribute to the maintenance of these ecosystem processes, watershed protection and the maintenance of the country's cultural heritage. The network would include the array of protected area management categories needed to meet Guyana's national objectives for biodiversity conservation and sustainable use of natural resources and would assist Guyana to make substantial progress towards achieving levels of representation of major ecosystems consistent with the international norms defined by the World Commission on Protected Areas of IUCN – The World Conservation Union, and other bodies (Government of Guyana 1998). International donors and the international community willingness to help Guyana pay for and maintain a network of protected areas have been overwhelming (Government of Guyana 1998). One of the main hurdles to the establishment of a network of protected areas in Guyana is, however, determining the location of priority conservation areas and the order of importance of these sites for setting up on-the-ground management. This thesis explores some of the options to overcoming this problem.

2.5 CONCLUSIONS

Much of the natural habitats of the Neotropics have been severely fragmented and have been altered by human interventions and settlements. The remaining intact areas are critical for the preservation of species and unique ecosystems, and serve as an invaluable scientific resource for understanding tropical ecology. Guyana is at a crucial juncture in its development. It is a sparsely populated country, with vast, near pristine, intact forests and great economic pressure to exploit its natural resources. The pressure on Guyana to diversify its economy and maintain above average growth is fuelled by severe poverty and large foreign debts. The easiest economic development opportunities lie with forestry and mining. Since very little land is privately owned in Guyana, the government has a great responsibility to ensure proper land use and that a sufficient amount of land is conserved in its natural state. These conditions create a need for a rationale and well-justified approach to designating conservation sites.

At the same time, with virtually no land under formal protection, Guyana is one of only a few countries left in the world that has the opportunity to design an entire protected area network specifically to conserve biological diversity. One of the largest hurdles to this challenge is measuring Guyana's biodiversity country-wide and determining which land should be exclude from extractive activities such as logging and mining and protected. The type of detailed biodiversity data required to make precise conservations plans are impractical and very costly at best. It is more likely that they are impossible to attain before Guyana's land use options expire. Rationale conservation plans must be based on the best available or readily available data.

With time a critical factor, decisions have to be made on where to put protected areas in Guyana to maximise the conservation of biological diversity, while minimising the potential loss of extractive natural resources. This real estate problem may sound simple enough, but as the chapters in this thesis will demonstrate, both the theoretical and practical underpinnings are complex. Although the conceptual framework presented in this thesis could be applied to conservation decision-making in any place and at any scale, the global opportunities to create new protected or conservation areas are limited. Guyana is in the rare position of being able to use such a framework to make decisions that could result in a globally significant protected area network representative of its critically important biological diversity.

Chapter Three

Literature Review and a Conceptual Framework for Conservation Decision-Making

3.1 INTRODUCTION

There is mounting pressure to create new protected areas to conserve biodiversity. A fundamental question is where should new protected areas be located to most effectively conserve biodiversity. The decision of where to place a new protected area ideally should be based on sound principles and criteria. Two practical considerations shape the answer to this question. First, land suitable for conservation may be in competition with other land uses such as agriculture or forestry. Secondly, the financial resources available to protect areas from threatening processes are limited, and may constrain the number and size of protected areas (Pressey 1997). Unfortunately, there is no 'recipe book' of criteria to follow on how best to designate new protected areas to conserve all elements of biodiversity, only emerging studies that demonstrate some of the principles and pitfalls (Flather *et al.* 1997).

Increasingly, decisions have to be made with incomplete information. Conservation decisions must then be based on the best information at that time. Deciding what is the 'best' information is a complex task. As mentioned in the introduction of this thesis (section1.1), biodiversity can be measured by several different surrogate measures at three organisational levels; ecosystem, species and genotypic (Noss 1990). Information from these three levels must be sorted and used in a systematic fashion to determine the location of new protected areas. The techniques for selecting *priority biodiversity sites*, those sites that contain representative samples of the biodiversity in a given area, have progressed considerably in the past twenty years and now integrate quantitative data, explicit conservation targets, and selection criteria (Pressey 1997). These techniques also allow for the evaluation of which areas need to be protected and which areas might be suited for other land uses (Ferrier 1997).

This chapter reviews the current literature relating to factors influencing observed patterns of biodiversity distribution, measurements of biodiversity, methods for selecting protected areas, issues regarding the spatial of analysis and choice of area with regard to other land uses. The chapter presents an overview of the above themes and a conceptual framework for conservation decision-making that incorporates the various themes.

3.2 PATTERNS OF BIODIVERSITY DISTRIBUTION

The distribution of biological entities worldwide is skewed. The majority of species live in tropical regions and prosper in diverse tropical ecosystems. Numerous hypotheses have been proposed to explain the distribution of biodiversity in a given area; however, no single factor has been found that explains all of the observed patterns of distribution (Fischer 1960, Connell and Orians 1964, MacArthur 1965, Pianka 1966, MacArthur and Wilson 1967, Pielou 1975, Terborgh 1977, Connell 1978, Huston 1979, Tilman 1982, Gentry 1988, Owen 1988, 1990, Currie 1991). Instead, several factors may act together to influence the diversity in any given area. The main factors hypothesised to influence the distribution of diversity and the function they play can be summarised as follows:

Factor	**Function**	**Source**
Climatic variability	Stability permits specialisation of species	Fischer 1960
Habitat heterogeneity/ Complexity	Physically or biologically complex habitats furnish more niches for species	MacArthur and MacArthur 1961, Terborgh 1977, Gentry 1988
Consistent environment	Lower extinction rates	Stebbins 1974
Time	More time permits more complete colonisation and the evolution of new species	Ehrendorfer 1970
Resource availability	Greater resource availability and predicability allow for greater specialisation	Pianka 1978
Competition	Competition favours reduced niche breadth	Terborgh 1977, Connell 1987
Predation	Predation retards competitive exclusion	Terborgh 1977, Connell 1987

Many researchers have tested these hypotheses and the results have lead to general descriptions of the patterns of distribution of biodiversity at several levels of scale. In most instances, the patterns of biodiversity are described at the species-level and ignore the distributional patterns of ecosystems and genotypes with the exceptions of Olson and Dinerstein (1998) for ecosystems and Moritz and Faith (1998) for genotypes.

3.2.1 Patterns of Biodiversity at the Global Scale

Global patterns of species distribution show that species richness, the number of species in a given area, increases with decreasing latitude (Fischer 1960, Pianka 1966, Cowling and Samways 1995). Terrestrial diversity reaches its peak in tropical rainforests and marine diversity reaches its peak in shallow-water benthic communities (Pianka 1966, Connell 1978). Tropical rainforests represent approximately 6% of the earth's surface, but are estimated to contain 50-90% of the world's terrestrial species (Myers 1988). The overall pattern of species increases with proximity to the Equator and masks several minor trends in particular habitats or taxonomic groups showing little or no increase in richness with decreasing latitude (Pianka 1966).

Species richness on a global scale also tends to increase with increasing precipitation (Connell and Orians 1964, Pielou 1975). The relationship between species richness and precipitation is most apparent at the extremes (tropical rainforests versus deserts). In the neotropics, plant species richness is positively correlated with absolute annual precipitation, however, this relationship is not as strong in the paleotropics (Gentry 1988).

Tree species richness appears to vary intercontinentally. In the temperate zones of the Northern Hemisphere there is a vast difference in the species richness of trees and shrubs. Temperate forests in East Asia have approximately 876 tree and shrub species. North American forests meanwhile have approximately 158 species and European temperate forests have approximately 106 species (WCMC 1992). This appears to be due to the historical biogeography of the different temperate areas (Gentry 1988). This pattern, however, does not hold true in the tropics. Gentry (1988) showed that equivalent forest types in South America, Africa, and Asia showed similar plant species richness and floristic composition, however, they differed remarkably in their structure.

3.2.2 Patterns of Biodiversity at the Continental Scale

Studies at the continental level are still rare. For North America, species richness for taxonomic groups of mammals, birds, reptiles, and amphibians was shown to vary strongly with latitude. However, potential evapotranspiration was shown to be the best predictor of species richness for birds, mammals, amphibians, and reptiles (Currie 1991). For trees, actual evapotranspiration was shown to be the best predictor for species richness (Currie and Paquin 1988). Similarly, primary production was shown to relate strongly with tree species richness in Europe and East Asia (Adams and Woodward 1989). More work needs to be done at the continental scale however, before general patterns can be established.

3.2.3 Patterns of Biodiversity at the Environmental Gradient Scale

At the environmental gradient scale, species richness decreases with increasing altitude (MacArthur 1965, Pianka 1966). This gradient is best demonstrated for extremes in altitude that are very species-poor. At low and middle elevations, the data on species richness are not as definitive, as other factors such as precipitation and solar radiation tend to influence species richness (Pianka 1966). However, Owen's (1990) study of mammalian species richness across Texas showed variance in elevation to be a strong predictor of species richness for bats and rodents.

Temperature, precipitation, and solar radiation have been shown to positively correlate with the richness of particular plants in California (Richerson and Lunn 1980). Likewise, Cowling *et al.* (1998) showed that the high regional plant richness for the Cape Peninsula in South Africa was a function of environmental heterogeneity, measured as a function of topography, annual rainfall and mean winter temperature. A detailed study of plant species richness along an elevational gradient of habitats in South America showed that when latitude and altitude were controlled for, plant species richness increased with increasing precipitation and soil fertility (Gentry 1988). These relationships also appear to hold true for birds, reptiles, amphibians, butterflies, and bats along the same habitat gradient (Gentry 1988).

Some observed patterns of species richness at the environmental gradient scale appears to be influenced by the density of canopy foliage, which may be considered to be a proxy measurement of habitat complexity, precipitation, and edaphic factors. For example, a comparison of bird species richness in four forest types (lowland rainforest, montane forest, cloud forest, and elfin forest) along an elevational transect in Peru showed that bird species richness was strongly correlated with the density of the canopy foliage, with the greatest richness in the lowland rainforest (densest canopy) (Terborgh 1977). A similar relationship between species richness and the density of canopy foliage along a gradient was found for birds in Panama (Karr and Roth 1971), birds in New Guinea (Kikkawa and Williams 1971) and desert rodents in the United States (Rosenzweig and Winakur 1969).

3.2.4 Patterns of Biodiversity on Islands

Island communities are generally poorer in species than comparable mainland communities. Studies have shown that the number of species on an island is positively correlated with the area of the island and the topographic diversity and negatively correlated with distance from source of immigrants on the mainland (Preston 1960, MacArthur and Wilson 1967). The ground work by MacArthur and Wilson on island biogeography (1967) and subsequent empirical tests have led to nearly three decades of research on the relationship between area and species. This relationship is commonly represented by species-area curves that plot the accumulation of species with increasing sample area. A wide range of studies shows this to be a consistent relationship (e.g. Arrhenius 1921, Gleason 1922, Darlington 1957, MacArthur and Wilson 1963, 1967, Preston 1960, Diamond 1973, Connor and McCoy 1979). Studies are well documented on oceanic islands, where the strongest correlations between species and area are found on islands of similar relief (Darlington 1957, Diamond 1973). But, studies on larger land masses and habitat patches, in particular protected areas, have provided mixed support for the relationship between the number of species and area.

An analyses of 100 species-area curves showed a positive relationship between area and species number, although there was no single best-fit model to explain this relationship (Connor and McCoy 1979). The species-area equation is typically expressed as species numbers and areas transformed logarithmically by the equation $S=Ac^{z}$, where S is the number of species, A the area, z is the slope and c is a fitted constant (Preston 1960, 1962 and MacArthur and Wilson 1967). The slope of the relationship (z) varies considerably between studies, however, it generally falls between 0.15 and 0.40 (Connor and McCoy 1979). The implication of this equation is that with a slope of 0.15, a tenfold loss of area will result in a 30% loss of species and with a slope of 0.40, a tenfold loss of area will result in a 60 % loss of species (Connor and McCoy 1979).

3.2.5 Patterns of Biodiversity at a Local Scale

Local scale patterns of biodiversity are considered by four measures, each reflecting a different level of biological organisation: point-diversity (representing diversity at a single point); alpha-diversity (the number of species in a small, homogenous area); beta-diversity (between habitat diversity); and gamma-diversity (diversity across a landscape) (Whittaker 1965). Alpha diversity is measured as: $Aj = \max [aij]$, where aij is the richness of the habitat i ($i=1,\ldots,n$) in sampling unit j. Beta diversity is measured after Whittaker (1977) as:$Bj = Sj \sqrt{a}\ ij$ where $\sqrt{a}\ ij$ is the average number of species in the habitats i ($i = 1,\ldots,n$) in sampling unit j, and Sj is the total richness in sampling unit j. A value of beta diversity close to 1.0 indicates a single habitat type. Since alpha diversity is the diversity of a homogenous area, the biodiversity of the area is strongly correlated with physical environmental variables (Margurran 1988). As spatial scale is broadened, other habitats are included and thus beta-diversity reflects the combination of habitat types and environmental gradients (Margurran 1988). The gamma diversity incorporates even more habitat types than beta diversity, thus diversity is again increased with spatial scale. A few studies have looked at the contribution of alpha and beta diversity to the overall diversity of an area (*e.g.* Harrison *et al.* 1992, Lawton *et al.* 1994). Harrison *et al.*'s (1992) study showed that beta diversity was relatively low compared with alpha diversity for birds species in Britain. Lawton *et al.* (1994) showed variation in the alpha diversity across Britain and very low corresponding beta diversity for the same areas. They concluded that in temperate areas, the majority of biodiversity may be captured in a small number of large areas with high alpha diversity, however, they hypothesised that a different strategy may be necessary for the tropics (Lawton *et al.* 1994). Tropical habitats tend to contain more species and a high proportion of endemic species, but do so in smaller geographic ranges. Thus, areas of the same size in the tropics most likely have a higher beta diversity than similar areas in temperate regions (Lawton *et al.* 1994).

What is striking about all of these patterns of species distribution, is the complexity of factors that influence biodiversity patterns. Singling out one factor that could be used as a surrogate for the *amount* of biodiversity in a given area is difficult and scale-dependent. Instead, researchers have tended to try to measure the actual biodiversity in a given area using various surrogate measures.

3.3 SURROGATE MEASURES OF BIODIVERSITY

There are three main types of spatial data that are used as surrogate measures of biodiversity. They include: a) land classifications such as vegetation maps; b) derived or modelled environmental domains (classifications of abiotic environmental variables based on numerical pattern analysis); and c) species data (recorded and modelled) (Belbin 1995, Margules and Redhead 1995, Ferrier 1997). These surrogate measures, when used alone or in combination, provide a geographically complete map of the abiotic or biotic variables likely to be correlated with the distribution of the elements of biodiversity (Ferrier 1997).

3.3.1 Vegetation Maps

As discussed in section 3.2.3, precipitation and elevational gradients are correlated with species richness. One of the easiest ways of classifying these gradients is to use vegetation maps. Vegetation types can usually be divided along precipitation and elevational gradients from wettest and lowest (rainforest) to driest (deserts) and highest (elfin woodland) and can be useful as a surrogate for species richness and ecosystem types (Meffe and Carroll 1994). In addition, the density of canopy foliage was correlated with species richness in some instances (section 3.2.3). Vegetation maps derived from air photos or satellite images and subsequently ground thruthed usually reflect difference in the density of canopy foliage, as well as precipitation and elevational gradients and can be used as a surrogate measure of biodiversity (Margules and Redhead 1995). Although, the classification of vegetation types is somewhat arbitrary, it can be very useful as a surrogate measure of biodiversity, as it is readily available in most countries.

3.3.2 Environmental Domains

As mentioned above and in section 3.2.3, precipitation, elevation and soil fertility are correlated to species richness. These variables and other important climatic and topographic variables, such as temperature and slope, can be used to generate environmental classes or domains. Mapped and modelled environmental variables can be classified into environmental domains using numerical pattern analysis techniques (Ferrier 1997). The pattern analysis techniques used include non-hierarchical cluster analysis (Belbin 1993a), and ordination (Faith 1991, Faith and Walker 1993, 1996a). These techniques break the range of variation in variables down into discrete and complementary groups and then use these groups as surrogate 'units' of biodiversity. Different environmental domains are assumed to support different suites of species and can be used as a surrogate measure of biodiversity (Margules and Redhead 1995). Like vegetation maps, abiotic environmental data variables are more widely available in most countries than species distribution data.

3.3.3. Estimated Species Data

Although biodiversity can be measured at higher organisational levels (e.g. ecosystems), species lists are the most common method of recording biodiversity at a given site. Species lists provide good guidance for representativeness but may miss genetic and ecosystem variability. Moreover, field surveys can only record a fraction of the species at any given site. They are usually confined to a few transects within a survey site, a few taxonomic groups (e.g. birds, mammals and vascular plants) and are often only conducted once. These constraints create geographical, taxonomic, and temporal gaps in the data (Ferrier 1997). Several techniques have been developed to deal with these gaps. They include: a) modelling known species records on biophysical data to create a geographically complete map of recorded and predicted species distributions; b) using 'indicator' taxonomic groups to represent other taxonomic groups; and c) using existing and/or historic data from museums and herbaria and experts to supplement recent field surveys (Margules and Redhead 1995, Ferrier 1997).

3.3.3.1 Predictive Modelling of Species

Relating direct species survey data to environmental variables to obtain a predictive model of the biological distribution of a species is a technique that has been widely employed over the last two decades (Nix 1982, Nix 1986, Austin and Margules 1996, Margules *et al.* 1988, Scott *et al.* 1988, Walker 1990, Lindenmayer *et al.* 1991, Nix and Switzer 1991, Carpenter *et al.* 1993, Butterfield *et al.* 1994, Margules and Austin 1994, Scott *et al.* 1993). Predictive modelling of species assumes that differences in species composition and abundance at any given location can largely be explained by differences in environmental factors, such as temperature, moisture, nutrients and evaporation (Nix 1982, Austin *et al.* 1984, Busby 1986, Margules *et al.* 1988, Currie 1991, Lindenmayer *et al.* 1991, Wylie and Currie 1993, Butterfield *et al.* 1994, Belbin 1995). Predictive species modelling can be: a) intuitive, based on local or expert knowledge of a species distribution in relation to environmental variables or land classifications (e.g.

distribution maps of species found in field guides); b) empirical, based on matching environmental variables with known presence records of species; or c) statistical, based on detailed presence/absence species data that is correlated to environmental variables (Nix 1982, Austin *et al.* 1984, Busby 1986, Margules *et al.* 1988, Butterfield *et al.* 1994, Belbin 1995). In addition to increasing the geographical coverage of a species' likely distribution, predictive modelling can be used to remove some of the sampling biases when species records are collected from opportunistic and easily accessible sites (e.g. road and river sides).

3.3.3.2 Indicator Taxonomic Groups

Indicator taxonomic groups are those groups of species that are typically well studied and more easily accessible (Prendergast *et al.* 1999). Commonly used indicator groups include mammals, birds, vascular plants, butterflies, reptiles and amphibians. The rationale behind using indicator taxonomic groups is that areas that are species-rich for a well-studied taxonomic group should be species-rich for lesser known groups (Landres *et al.* 1988, Pearson and Cassola 1992, Prendergast *et al.* 1993, Lawton *et al.* 1994). Cross-taxon congruency, or the amount of spatial overlap between the distribution of different taxonomic groups, has been examined in several studies and most studies have demonstrated poor to moderate correspondence of species richness among taxonomic groups at spatial scales relevant to conservation decision-making (e.g. Prendergast *et al.* 1993, Lawton *et al.* 1994, Howard *et al.* 1998, Pimm and Lawton 1998,Van Jaarsveld *et al.* 1998). At large geographic scales (e.g. continental), it is assumed that most terrestrial taxa are governed by similar biogeographic influences and carefully selected taxon could be used to represent the distributional patterns of other taxa (Pearson and Carroll 1998). Although cross-taxon congruency is interesting from a biogeographic perspective, congruency of species distribution patterns at the spatial scale of conservation decision-making may not be as important as whether the indicator taxonomic groups used captures a large portion of the species from other taxonomic groups (Balmford 1998). For example, if the sites that are the most species-rich for birds do not correspond exactly with the sites most species rich for mammals, but the bird sites collectively capture 85 % of the mammal species, they could be considered to be a good surrogate measure for mammals. Although there have been several studies examining cross-taxon congruency, only two have been in tropical areas (Uganda and South Africa) and both were carried out in Africa. To date, no study using neotropical or Asian data has been published.

3.3.3.3 Data Sources

Field surveys of species can be supplemented with existing species records from museum collections and herbaria. Museum and herbaria records are usually specimen-based and are often geo-referenced, thus providing information that can help fill the geographical and temporal gaps in the field survey data. Caution must be used with old data, as habitat modification may have altered or eliminated the species at a particular location.

Another way that has been postulated to get around the lack of species-level data to measure biodiversity has been to use higher-taxon richness as a surrogate for species richness (Williams 1993, Williams and Gaston 1994, Balmford *et al.* 1996a,b, Gaston and Williams 1996). Balmford *et al.* (1996a) investigated the use of higher taxa in angiosperms, birds and mammals in the Indo-Malaya and Pacific Rim area, and found that the total species richness of sites for each group was positively (although the strength of the relationship varied) related to genera, family and order richness. They concluded that depending upon the taxonomic level considered, data on higher taxa could be a valuable surrogate for species richness, especially in tropical areas where species data are costly and difficult to obtain. However, these relationships have yet to be tested for other areas of the world or on finer spatial scales.

Once surrogate measures on biodiversity have been compiled, sites that warrant protection within a country or region have to be identified. Identification of sites involves: a) defining clear criteria by which sites will be identified (*i.e.* measures of biodiversity); and b) stating an explicit conservation goal or target (*i.e.* the amount of biodiversity that needs to be protected). In general, sites that are set aside to protect biodiversity should encompass: a) sites rich in species; b) sites that retain ecological processes; c) ecosystems generally under-represented elsewhere; and d) sites that support rare or endangered species (Primmack 1993). There are many criteria that can be used to identify such sites. These include environmental/ecosystem representativeness, species-richness, concentrations of species that are geographically restricted, and measure of uniqueness or 'irreplaceability' (Myers 1988, 1990, Mittermeir and Werner 1990, Pressey *et al.* 1993, Scott *et al.* 1993, Butterfield *et al.* 1994, Reid 1998, Prendergast *et al.* 1999). Among these criteria, species richness is most commonly used to identify priority biodiversity sites that need conservation (Prendergast *et al.* 1999).

The goal of most protected area networks is to represent the biodiversity of a region or country. In practice, this goal is translated into the representation of the surrogate measures of biodiversity a nominated number of times or with a nominated proportion of area. Along with quantitative measure of biodiversity and conservation targets, the selection of areas within a protected area network should be based on transparent and repeatable methods that are cost-effective (Pressey *et al.* 1993, Pressey 1999). These underlying principles of conservation decision-making have been incorporated into several systematic protected area selection methodologies (Pressey 1997).

3.4 METHODS FOR SELECTING PROTECTED AREAS

The past twenty years have witnessed considerable progress in moving from *ad hoc* methods for selecting priority biodiversity sites that lacked explicit goals to systematic protocols that identify sets of priority biodiversity sites for a protected area network based on explicit criteria. However, the development of explicit criteria has taken a long time and criteria have come from diverse ideas on setting priorities from examples worldwide, only some of which have been retained by the systematic conservation decision-making approaches employed today (Pressey 1997). The initial systematic approaches were based on scoring or rating several criteria to produce an overall indication of the priority of different sites for conservation (Pressey 1997). These approaches were replaced in the 1980s by a "minimum set" approach, which moved away from scoring the 'value' of individual sites and concentrated instead on combining areas to form the best 'network of protected areas' (Kirkpatrick 1983, Pressey *et al.* 1993). In trying to look at the bigger picture, minimum set approaches attempted to represent an explicitly stated quantitative target of biodiversity (e.g. 10 % of each vegetation type or 2 occurrences of each species) in the most efficient manner (Kirkpatrick 1983, Ackery and Vane-Wright 1984, Austin and Margules 1986, Vane-Wright *et al.* 1991, Pressey *et al.* 1993). The incorporation of the concept of "representativeness" in the minimum set approach meant that priority biodiversity sites were selected that were complementary in nature, with each new site attempting to represent what was not already represented in existing protected areas (Vane-Wright *et al.* 1991, Pressey *et al.* 1993, Margules *et al.* 1994). Five features distinguished the minimum set approach from previous *ad hoc* approaches (Margules *et al.* 1994, Pressey 1999). Minimum set analyses are:

> a) *Target-directed.* In order to select areas, an explicit quantitative target of representation has to be stated. This target can be expressed in many ways such as a percent of land, a percent of each ecosystem or a number of occurrences of each known species.
>
> b) *Data-driven.* The selection of areas using a minimum set approach requires data on the distribution of biodiversity in the areas under consideration. These data are taken from the various measures of biodiversity and are stored in a matrix of biodiversity feature by area.
>
> c) *Efficient.* Minimum set analyses are designed to achieve a stated target with the minimum amount of cost. Cost being measured as number or size of protected areas or the opportunity costs of other land use activities.
>
> d) *Flexible.* Protecting certain sites may be impossible due to conflicting land uses thus, a range of possible alternatives may be sought. Where possible, flexibility in site location should be built into site selection.

e) *Transparent and repeatable.* The results of a minimum set approach should be explained in terms of targets and data used and should be repeatable by any number of people.

3.4.1 Selection Algorithms

The most common minimum set analyses are carried out using stepwise, or iterative algorithms that apply a sequence of rules based on a specific predetermined target to find the most appropriate site (Kirkpatrick 1983, Margules *et al.* 1988, Pressey *et al.* 1993). Once a site has been selected, the algorithm recalculates the potential contribution of all the other sites and selects the next most appropriate site until every feature is represented to meet the target (Pressey *et al.* 1996). This systematic approach allows for sites to be selected that are highly complementary in nature (eliminating unnecessary duplication) and highly efficient (Pressey and Nicholls 1989a,b).

Iterative minimum set algorithms are heuristic and as noted by a number of authors, they may not always find the most optimal solution (Vane-Wright *et al.* 1991, Underhill 1994, Camm *et al.* 1995, Church *et al.* 1996, Pressey *et al.* 1995, Williams *et al.* 1996, Csuti *et al.* 1997, Pressey *et al.* 1997). Optimal approaches using integer programming algorithms have been developed and have been shown to be useful when the number of potential protected area is large or the representation goal is complex (Church *et al.* 1996, Williams *et al.* 1996). For most protected area selection, the processing time using optimal algorithms is too large. Sub-optimal heuristic algorithms can usually be run in a matter of seconds and can provide indicative answers to the representation goal, while implementing the principle of complementarity (Pressey 1997, Freitag and Van Jaarsveld 1998). Several studies have compared different protected area selection algorithms (Csuti *et al.* 1997, Freitag *et al.* 1997, Pressey *et al.* 1997, Freitag and Van Jaarsveld 1998) and in spite of their common approach, no single algorithm was found to be appropriate for all planning scenarios. Instead, it appears that the most appropriate algorithm is dependent upon the objectives of the protected area network (Kershaw *et al.* 1994, Freitag *et al.* 1997, Prendergast *et al.* 1999).

3.4.2 Gap Analysis

Most countries and regions have an existing protected area network. Protected areas selection algorithms are usually used to select additional protected areas or modify the size/shape of existing protected areas. One of the most useful means of identifying and measuring to what extent a representation goal or target has been achieved in the existing protected areas, is to perform a gap analysis. Gap analysis, developed for conservation decision-making in the United States, uses geographic information systems (GIS) to identify sites that warrant protection, but currently fall outside of the existing network of protected areas (Burley 1988, Scott *et al.* 1993, Caicco *et al.* 1995, Kiester *et al.* 1996). Vegetation classes and actual vertebrate species ranges, mapped on irregularly shaped hexagons at a scale of 640 km^2, are used to model species distributions (Butterfield *et al.* 1994, Keister *et al.* 1996). Existing reserves are then mapped onto the distributional hexagons to determine if a species under consideration is adequately protected. The 'gap' of unprotected species is then used as the basis to select additional protected areas using protected area selection algorithms (Davis and Stoms 1996, Keister *et al.* 1996). Similar applications of protected area selection algorithms have been used in Australia and South Africa to designate new areas for protection (e.g. Kirkpatick 1983, Pressey and Nicholls 1989a, Rebelo and Siegfied 1992, Nicholls and Margules 1993, Pressey *et al.* 1994, Lombard *et al.* 1997, Pressey 1997, Freitag and Van Jaarsveld 1997). In all of the above cases, different selection algorithms were used, however the systematic approach was the same.

One of the limitations of protected area selection algorithm that has arisen after years of application, is that they do not provide a means to interpret which areas have the ***highest*** conservation priority (Pressey 1997). Selection of areas is done to meet an overall target with little regard to the order with which they need to be conserved. Knowing the order of priority becomes a critical issue if a country or region is limited in the number of protected areas it can establish at one time. Very few countries are in the position of being able to protect and manage an entire network of protected areas at once, hence ranking areas in terms of their 'irreplaceability" within the network becomes important. A recent outcome of selection algorithm research is the application of the concept of "irreplaceability" to the selection procedure (Pressey *et al.* 1993).

3.4.3 Irreplaceability

The irreplaceability value of an area refers to the importance of the area for achieving an explicit conservation target (e.g. the representation of 10 % of each vegetation type) (Ferrier *et al.* in press). Once the conservation target has been nominated, irreplaceability values can be calculated and used within selection algorithms to determine priority biodiversity sites. Used in this context, irreplaceability can be defined as the likelihood that the site will be required as part of a network of protected areas that achieves a set target, or the extent to which the options for achieving a set of targets are reduced if the site is unavailable for protection (Pressey *et al.* 1993, Ferrier *et al.* in press). Irreplaceability can then be measured on a scale of 0-100 % irreplaceable. If a site is totally irreplaceable (100%) then no matter how many options there are to achieve a set target, the network will have to include that site. Sites with progressively lower irreplaceability values have more and more replacements within the area under consideration, and sites with an irreplaceability value of zero contain features that have already met their target in existing protected areas (Pressey 1999). Each time a priority biodiversity site is protected, the irreplaceability values of the remaining sites can be recalculated. This approach has been used to select protected areas in Australia, South Africa and the United States (Pressey *et al.* 1993, Rebelo 1994, Pressey 1994, Lombard *et al.* 1997, Davis *et al.* 1999, Lombard *et al.* 1999). Although the concept of irreplaceability is straightforward, the measurement of irreplaceability depends on the biodiversity features in the area, the conservation target, and how many other areas contain each of the features of biodiversity (Pressey 1999). The statistical approach for predicting irreplaceability has recently been refined and the computational speed increased (Ferrier *et al.* in press). When multiple features of biodiversity are used (e.g. several species, vegetation types or environmental domains), an index of summed irreplaceability can be used, which is the sum of the irreplaceability values for a given site (Pressey *et al.* 1994, Ferrier *et al.* in press). A new interactive software package called C-Plan (NWS NPWS 1996) that runs as an extension in ArcView, can be used to calculate irreplaceability and summed irreplaceability values.

One of the strengths of systematic protected area selection is that it can be applied at any geographical scale from continents to individual protected areas using data at the appropriate resolution for the area being analysed (Margules and Redhead 1995, Pressey 1999). One of the main issues emerging from studies comparing methodologies of protected area selection is that the spatial scale of investigation is important. Measurements of biodiversity are often made at a different spatial scale from the spatial scale at which conservation decisions are made (e.g. the total number of birds recorded for a country may be used to decide where to place a protected area within a watershed). Recent studies have shown that assumptions used routinely in conservation decision-making regarding measurements of biodiversity (*i.e.* cross-taxon congruency and overlap of species-rich and endemic areas) only hold true at specific, usually coarse, spatial scales (Flather *et al.* 1997, Reid 1998). The role of spatial scale has generally been ignored in conservation decision-making, primarily because the spatial and temporal distribution of species is still relatively poorly understood (Wiens 1989).

3.5 ROLE OF SPATIAL SCALE

Scaling issues are fundamental to all ecological investigations. There are two types of scaling issues important in measuring biodiversity and conservation decision-making: 1) those relating to the elements of scale which are inherent, such as the physical differences between a species and an ecosystem; and 2) those relating to perceived elements of scale, or the scale-of-observation. These have no biological manifestation, but influence the way biological phenomena are perceived.

3.5.1 Scaling Theory

Systems ecologists generally consider the organisation of the environment in terms of a hierarchy. The most common levels of an organisational hierarchy in ecology consist of individuals, populations, biotic communities, ecosystems, landscapes and biomes (Colinvaux 1986, Odum 1989, Noss 1990). An important consequence of hierarchical organisation is that as phenomena are combined to produce larger functional wholes, new properties emerge which were not present or evident at the lower level and which are a result of the functional interactions of the phenomena at the higher level (Allen and Starr 1982, O'Neill *et al.* 1988). Studies of biological hierarchy show examples of both regional phenomena constraining local phenomena and local patterns constraining regional patterns (Allen and Starr 1982, Wiens 1989). Global and regional patterns of biodiversity may have their origin in and influence finer-scale phenomena. Because the effects of local heterogeneity are averaged out over larger areas, ecological patterns may appear to be more predictable at broader scales (Wiens 1989). For instance, local demographic instability of a population that may arise from microhabitat differences may translate over larger areas into long term stability of a population. In addition, the relationships between climate and vegetation that are evident at broad scales may be overridden at finer scales by competition and other biological processes such as edaphic and microtopographic factors (Woodward 1987, Wiens 1989).

Scaling theory argues that distribution patterns are highly dependent upon the resolution at which they are measured (Wiens 1989). One of the most important debates in the literature surrounding scaling and hierarchy theory revolves around the question of whether the scale spectrum of ecological systems is continuous, with every change in scale bringing with it changes in patterns and process. If the scale spectrum is not continuous, discrete ranges of scale may exist over which for a particular phenomenon in a particular ecological system patterns do not change. It is postulated that if discrete ranges of scale exist, they may be separated by relatively sharp transitional areas where the dominance of one set of factors switches to the dominance by another set and where they may exhibit unpredictable behaviour at the transition (O'Neill *et al.* 1988, Wiens 1989, Meentemeyer and Box 1987). Support for a scale spectrum that is not continuous comes from the study of ecology where ecosystems are viewed as a composite of discrete lower levels of organisation, individuals and populations. The nature of a community and an ecosystem is considered to be more than just the sum of the species with in it; it is also the sum of their interactions (Odum 1989). If discrete ranges of scale do exist for a known phenomenon, then findings at a particular scale may be extrapolated to other scales within the range, but extension between ranges may be difficult. However, correlations among variables that are evident within a discrete range may disappear or change when the scale is increased above or below this range (Wiens 1989). These deliberations are complicated by the fact that the existence of ranges may be dependent on the phenomenon being considered.

3.5.2 Patterns and Spatial Scale

Most ecologists have studied biological phenomena on spatial scales that satisfy their experimental needs. A large number of ecological studies are conducted in small areas. For example, 60% of ecological studies surveyed in major biological journals were carried out on a spatial scale of less than one m^2 (Kareiva and Andersen 1988, Swanson and Sparks 1990). From the review of the observed patterns of biodiversity at fixed spatial scale (*e.g.* global, continental), it is clear that different trends are apparent at different levels of observed scale and that little research has been done to test whether patterns at one scale translate to another scale (Pianka 1966, Currie 1991). The scale of investigation may have profound effects on the patterns one finds (Wiens 1989). Wiens (1989) suggest that the ability to detect patterns that hold true at various spatial scales is a function of the extent (overall area of a study) and the grain (size of the individual units of observation or measurement) of investigation. Wiens (1989) argues that if the extent of an investigation is held constant, then increasing the grain of measurement generally decrease spatial variance, as a greater proportion of the spatial heterogeneity is contained within the grain.

For instance, species richness is a function of extent and grain measurements. The species richness of a local community is influenced by local speciation and extinction, but also by broader biogeographic dynamics. If species richness is measured by the presence or absence of a species, as grain size increases, more rare species will be recorded in each grain and species richness will increase (Wiens 1989). If grain size is held constant, increasing the extent of the study will tend to incorporate more spatial heterogeneity, which in turn will tend to increase the diversity between grains (beta diversity) and may increase the overall diversity (Wiens 1989).

Studies by Stoms (1994), Pressey and Logan (1995, 1998) and Davis and Stoms (1996) have altered the extent or grain size and look at the influence of extent and grain size on the species richness and location of the richest sites within an area. Pressey and Logan (1995, 1998) showed that the finer the geographic scale biodiversity is measured at, the more efficient protected area selection algorithms are at representing the biodiversity to satisfy a conservation target. If representing biodiversity at finer and finer scales means that the biodiversity can be represented in smaller and smaller land parcels, the viability of very small areas to conserve biodiversity in the long-term must be questioned. Although there is no minimum size for a protected area, population viability analysis has demonstrated that protected areas smaller than 10,000 ha. are unsuitable for the long-term persistence of most plants and animals (Schonewald-Cox 1983, Shafer 1990).

Areas smaller than 10,000 ha. may also limit ecological and evolutionary processes.

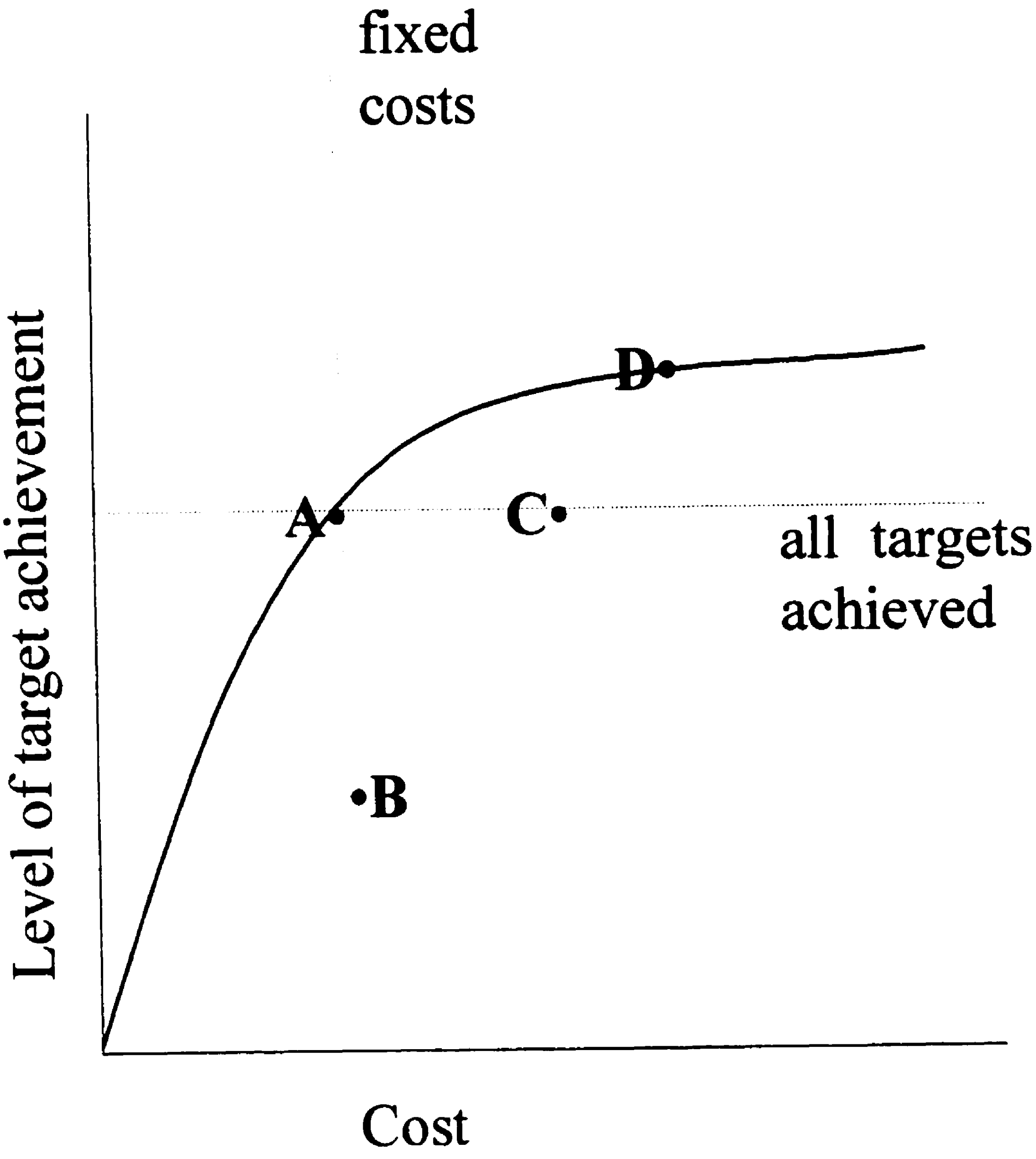
Assessments of patterns of biodiversity measures do not shed much light on the underlying biogeographic and evolutionary processes that a network of protected area is attempting to conserve, however, conservation of the interspecific interactions that drive these processes is critical (Cowling *et al.* 1999). Patterns of cross-taxon congruency at any particular spatial scale may reflect a common biogeographic history, or just the scale of investigation. A common pattern of biogeography depends upon either the inclusion of many environments, each with a distinct evolutionary history; or a homogeneous system with a common history of speciation, extinction and dispersal (Schneider and Moritz 1999). Even though for most regions, the underlying biogeographic patterns are not known and evolutionary processes (e.g. dispersal, speciation) are difficult to assess, this does not mean that they should not be considered in conservation decision-making. One point of debate is whether priority should be given to sites that contain ancestral taxa with evolutionary potential (Linder 1995), or to sites that represent the 'evolutionary' fronts of currently speciating taxa (Brooks *et al.* 1992, Moritz 1995).

Designing a protected area network to conserve both ecological and evolutionary processes may seem a near impossible task with the limited data and knowledge available, however, recent attention has been given to systematic selection processes that consider the long-term retention and persistence of biodiversity (Cowling *et al.* 1999). This is done in part by incorporating spatial design elements (such as size, shape and adjacency rules) and measures of threat to assess the vulnerability of different priority biodiversity sites (Cowling *et al.* 1999). If priority biodiversity sites are going to persist in the long-term and continue on-going evolutionary processes, there has to be some assessment of the urgency with which a site should be protected so a to maximise the number of biodiversity features that can be retained (Pressey 1997).

3.6 EVALUATING OPTIONS FOR BIODIVERSITY CONSERVATION

In an ideal world, all sites identified to be important within a protected area network would be conserved. Unfortunately, there are many land uses (e.g. agriculture, forestry) competing with biodiversity protection. Systematically incorporating other land uses into conservation decision-making is a relatively recent development, however, most protected areas around the world are the result of decisions made in favour of other land uses and thus, by default conservation decision-making has always recognised other land uses (McNeely 1994). There are two approaches to dealing with the integration of other land uses into conservation decision-making and they are not mutually exclusive. The first is to assess potential and possible threats to biodiversity conservation by devising an index of how vulnerable identified priority biodiversity sites are to those threats (Pressey 1997). The second approach, is to treat other land uses as a necessity and try and minimise the potential loss of the other land uses while maximising the amount of biodiversity conserved in a trade-off (Faith and Walker 1996a,b, Faith *et al.* 1996). This approach can be viewed as a cost-benefit analysis where the 'cost' is the loss sustained by the other land use (e.g. forgone wood resources) when land is given over to biodiversity protection and the 'benefit' is the amount of biodiversity that can be conserved as measured by the level of achievement towards a conservation target or goal (Figure 7). The ideal point is point A (Figure 7) where all targets are achieved and costs are minimal. Other points (e.g. B, C or D) either fail to achieve the level of protection target or have unnecessary costs (Figure 7). The main disadvantage to this approach is that the trade-offs are done without excluding those sites that are irreplaceable and all sites are treated equally with respect to the importance of the biodiversity they contain. If priority biodiversity sites exist that are irreplaceable or near irreplaceable, weighing their vulnerability to other threats appears to be a more reasonable approach.

Figure 7: Cost-Benefit of Protection - Point A is the ideal point in terms of achieving a conservation target with minimum cost; point B fails to achieve the conservation target; point C has unnecessary costs; and point D over-represents the target and has unnecessary costs.



Devising indices of vulnerability and incorporating them into conservation decision-making has recently occurred in Australia where timber and agriculture compete with biodiversity conservation (Pressey 1997). Although these indices may be oversimplifications of complex land use problems, they are a real step forward in integrating conservation decision-making with other land use planning. The widespread use of these approaches will occur further through studies and tests of how consideration of other land uses alters or influences the location of protected areas.

3.7 CONCEPTUAL FRAMEWORK FOR CONSERVATION DECISION-MAKING

The themes presented in this chapter can be summarised in a conceptual framework for conservation decision-making. This framework is based on:

1. Assessing and applying the most appropriate measures of biodiversity for a given area. This should be based on the best available data, hopefully spanning all three hierarchical levels of biodiversity.

2. Establishing clear and explicit criteria on how to treat the data and on representative targets for the establishment or expansion of a protected area network.

3. Employing a systematic selection method that is transparent, efficient, flexible and complementary in nature and incorporates some valuation of the priority with which sites should be protected (*i.e.* irreplaceability value).

4. Determining and applying an appropriate spatial scale of analysis.

5. Incorporating evaluation mechanisms, such as indices of vulnerability, so that sites can be temporally prioritised and re-evaluated if other land uses conflict with priority sites.

The application of this conceptual framework and the exploration of several of its assumptions are carried out in the remaining chapters of this thesis using data from Guyana. The widespread application of this framework to conservation-decision making is clear, from its adaptability to a variety of data and conservation targets.

Chapter Four

Biophysical Measurement of Biodiversity in Guyana

4.1 INTRODUCTION

The notion that biodiversity can be defined as a "nested hierarchy" of ecosystems, species and genes has given rise to various means of measuring and representing biodiversity (Noss 1990). Mapped land classifications such as vegetation maps and abiotic environmental variable maps have generally been used to represent ecosystems and habitats. Over the past several decades, governments, planners, conservationists and other scientists have argued that new protected areas should be located in areas that retain the greatest number of species. This "species-centric" approach has been the focus of most regional and global conservation strategies (Mittermeier and Werner 1990, McNeely *et al.* 1990, Bibby *et al.* 1992, WCMC 1992). This approach ideally requires extensive knowledge on the distribution of species. However, countries and regions often have inadequate databases on species distributions and thus have to rely on surrogate measures of biodiversity (Belbin 1993a). In most cases, as discussed in chapter 3, surrogates measures of biodiversity have either been environmental variables (Mackey *et al.* 1988, 1989, Bedward *et al.* 1992, Richards *et al.* 1990, Lewis *et al.* 1991, Belbin 1993a, Pressey and Tully 1994) or indicator taxonomic groups (Mittermeier and Werner 1990, McNeely *et al.* 1990, Bibby *et al.* 1992, Prendergast *et al.* 1993, Lawton *et al.* 1994, Dobson *et al.* 1997, Howard *et al.* 1998, Van Jaarsveld *et al.* 1998).

Surrogate measures of biodiversity derived from environmental or biophysical variables (e.g. ecosystem classifications, vegetation classes or environmental domains) incorporate information such as climatic data, soil attributes and terrain data and are easier and cheaper to acquire than species distribution data (Belbin 1993a, Pressey and Logan 1995, Hutchinson 1995). Using these types of surrogates assumes that by representing them in a protected area network, the species found within each surrogate class will be protected (Purdie *et al.*, 1986, Belbin 1993a, Faith and Walker 1995). Although this assumption has only been tested in limited instances (see Kirkpatrick and Brown, 1994 and Ferrier and Watson 1997), the use of these types of surrogate classes is widespread. Examples include: climatic attributes/environmental domains (Mackey *et al.* 1988, Bedward *et al.* 1992, Richards *et al.* 1990, Lewis *et al.* 1991); climatic and edaphic variables (Belbin 1993a), landscapes (Noss 1983, 1987, Scott *et al.* 1988, 1991, Pressey and Nicholls, 1989a), land systems (Purdie *et al.* 1986, Pressey and Nicholls 1989, Pressey and Tully 1994), and landscape ecosystems (Lapin and Barnes 1995).

This chapter is divided into three main sections. The first section describes some of the biophysical variables for Guyana. Although data are available from climate stations distributed around Guyana, geographically complete climate surfaces of Guyana do not exist. Several climate surfaces (rainfall and temperature) are created and presented in this chapter using spatial interpolation techniques. These surfaces are then used in conjunction with other abiotic variables to classify environmental domains. Similarly, the existing digital elevation model (DEM) of Guyana, created by the United States Geological Survey (USGS), is corrected using spatial interpolation techniques and used in this chapter. The second section uses the modelled climate and terrain data in combination with mapped substrate data to derive environmental domains using clustering techniques. In the third section, environmental domains are used as surrogate measures of biodiversity and are incorporated into a protected area selection algorithm to determine priority biodiversity sites. Maps of the location of priority biodiversity sites are compared for different environmental domain classifications and different conservation targets. A readily available vegetation map, drawn by Huber *et al.* 1995 from LANDSAT images, is then used as a surrogate measure of biodiversity and priority biodiversity sites are determined using the same algorithm and conservation targets as for environmental domains. The locations of priority sites from environmental domains and vegetation classes are compared. This chapter contributes to understanding the patterns of climates, terrain and substrate in Guyana and how those patterns, once translated into classifications based on clustering of environmental domains or vegetation classes, perform in the selection of priority biodiversity sites. Very few comparisons have been made of sites selected using environmental domains and vegetation class and fewer studies have examined sites selected using either environmental domains or vegetation classes with those chosen based on species distributions (Kirkpatrick and Brown, 1994 and Ferrier and Watson 1997, Wessels *et al.* 1999). None of these studies has been carried out in South America.

In addition, this chapter uses a novel approach to compare the performance of environmental domains and vegetation classes. An index of "irreplaceability" is used to determine priority grid cells in terms of their predicted biodiversity. The concept of irreplaceability was proposed by Pressey *et al.* (1993) and has been generally accepted in the conservation literature as being useful in determining priority biodiversity sites (Cowling1999, Davis *et al.* 1999, Pressey 1999). Using an index of irreplaceability, the performance of the different types of surrogate measures of biodiversity can be examined by selecting sites with the highest summed irreplaceability for one surrogate of biodiversity (*i.e.* vegetation type) and then looking at the percent of each of the other surrogates measures captured by those sites. By plotting the accumulation of the different features of the surrogate measure, a comparison can be made on how effective the other surrogates of biodiversity are at predicting the target-group, each other, and if they differ from selecting sites at random. This chapter uses this approach to compare the location of priority biodiversity sites for several derivations of environmental domains and vegetation classes.

4.1.1 Biophysical Biodiversity Surrogates

4.1.1.1 Climatic and Other Abiotic Environmental Variables

Several climatic and other abiotic variables, such as terrain, and substrate properties have been shown to correlate with the distributional patterns of species (Woodward 1987). Climate usually refers to mean monthly values for temperature and rainfall, solar radiation and soil moisture. Terrain variables include elevation, slope, aspect, relief and ruggedness; whereas substrate properties usually include lithology, soil depth, and soil fertility. Although the scale at which some of these variables correlate with species distributions may vary, combinations of climatic and other abiotic variables have been used as surrogate measures of species distributions (Austin *et al.* 1984, Margules and Stein 1989, and Nicholls 1989). In addition, several climatic variables, primarily ones based on rainfall, have been used as surrogates of primary production and other measures of vegetation productivity. Similarly, geology/lithology and soil maps have been used in lieu of vegetation maps (Austin *et al.* 1984). However, two phenomena have been observed when abiotic variables are used to describe the environment in which they occur: a) there tends to be a strong correlation between certain variables such as temperature and elevation, especially near the Equator; and b) many of the variables are autocorrelated (Ferrier and Watson 1997).

For any given area, the geographical and environmental space covered by the variables can be described by examining the relationship between each of the abiotic variables. These relationships can be used to classify similarities in both environmental and geographical space into "domains" and in turn, these "domains" can be used as explicit surrogates of biodiversity. In the case of Guyana, monthly mean rainfall and temperature data over many years are available. In addition, a digital elevation model (DEM) at a resolution of 1 km^2, the parent substrate type and an index of soil fertility are available. The importance of rainfall and temperature in determining the distribution of species has been widely demonstrated (e.g. Austin *et al.* 1984, Margules and Stein 1989, Nicholls 1989, and Lees and Ritman 1991). Terrain, parent substrate and fertility also have obvious importance, although the relationships have not been as clearly demonstrated.

4.1.1.2 Environmental Domains

Environmental domains are defined here as partitions of the abiotic environmental attributes of a given area into distinct categories or domains (Mackey *et al.* 1988). The use of environmental domains as surrogates of biodiversity is based on the belief that differences in species composition and abundance at any given location can largely be explained by differences in environmental factors, such as temperature, moisture availability, nutrients and evaporation (Nix 1982, Austin *et al.* 1984, Butterfield *et al.* 1994, Busby 1986, Margules *et al.* 1988, Currie 1991, Lindenmayer *et al.* 1991, Wylie and Currie 1993, Belbin 1995). Several classification methods have been used to derive environmental domains. The primary methods for generating domains are non-hierarchical cluster analysis (Belbin 1993b), and environmental ordination (Faith 1991, Faith and Walker 1993, 1996a). In these cases, environmental attributes are used to derive a multi-variate environmental space which reflects the statistical distance between areas of land of similar or different environmental character and the partitioning of land into relatively homogeneous areas (Faith 1991). These techniques break the range of variation in abiotic features down into discrete and complementary groups. The non-hierarchical cluster analysis algorithm most commonly used to create environmental domains uses a Gower metric, a statistical measurement of difference, to calculate the site-by-site surrogate distance matrix (Belbin 1991, 1993b). For studies using environmental ordination, a Gower metric is also used in a multi-dimensional algorithm (Belbin 1991). These algorithms can be run using a software package called PATN (Belbin 1993b).

Although studies in Australia commonly use both methods (Mackey *et al.* 1988, 1989, Richards *et al.* 1990, Kirkpatrick and Brown 1991, Lewis *et al.* 1991, Faith and Walker 1993, 1996a), the non-hierarchical clustering analysis is used in this study. A study on the effectiveness of environmental surrogates for data collected in New South Wales, Australia showed very little difference in results between the methodologies when the same data were used (Ferrier and Watson 1997), with the main difference being that for non-hierarchical cluster analysis the user defines the number of groups the data should be divided into. Non-hierarchical cluster analysis was chosen in this study so that the number of groups could be manipulated to compare with known vegetation classes. Environmental domains have been used to select priority biodiversity areas in north Queensland, Australia (Mackey *et al.* 1988), south-east New South Wales, Australia (Richards *et al.* 1990), Tasmania, Australia (Lewis *et al.* 1991, Kirkpatrick and Brown 1991) and Papua New Guinea (Nix *et al.* 1999).

4.1.1.3 Vegetation Classifications

Vegetation classifications from vegetation maps have also been used to select priority biodiversity sites (Diamond 1986, Scott *et al.* 1993, Shaffer 1996). Vegetation maps usually reflect differences in the underlying flora of a region and in particular, the canopy structure of forests. Maps depicting different vegetation classes can be used as a surrogate measure of biodiversity under the assumption that different vegetation classes reflect different ecosystem types, and by conserving a portion of each ecosystem, the plants and animals within each ecosystem will be protected (Shaffer 1996).

4.1.2 Irreplaceability

The shift away from species-based, *ad hoc* conservation decision-making policies has seen an increase in new methodologies that are data-driven and computer-based. One of the most important advances in conservation planning in recent years is the adoption of protected area selection approaches that are systematic in nature, data driven, goal-directed, efficient, transparent, repeatable and flexible (Pressey 1999). The methodology behind these systematic approaches is based on the conceptual framework described in chapter three. One of the outcomes of research into systematic conservation planning in recent years is the concept of irreplaceability (Pressey *et al.* 1993, 1994). As discussed in chapter three, the irreplaceability of an area can be defined in two ways: (a) the likelihood that it will be required as part of a conservation system that achieves the set of nominated targets; and (b) the extent to which the options for achieving the set of targets are reduced if the area is unavailable for conservation (Pressey *et al.* 1994). Irreplaceability so defined is not binary, rather it is a continuum of values for the areas in a region, from 100% to 0%. An area that is totally (100%) irreplaceable must be included in a system of conservation areas if all targets are to be achieved. By the same token, its loss (e.g. to clearing for logging) will cause one or more targets to become unachievable. Choices between sites with lower irreplaceabilities can be resolved according to location, size, condition, cost and other factors that influence the persistence of natural features and implications for ongoing management. In this chapter, the irreplaceability values of each grid cell is examined and compared for various combinations of environmental domains. Sites with high irreplaceability values are then compared for different environmental domain classifications and vegetation classes.

4.1.3 Priority Biodiversity Area Selection

4.1.3.1 Selection Algorithms

In recent years, systematic conservation planing has been based upon protected area selection algorithms that efficiently select a set of sites to achieve a nominated conservation target. As discussed in chapter three, there are several algorithms that have been used to systematically select priority biodiversity sites. The goal of these algorithms is to iteratively select sites to represent species or other surrogate measures of biodiversity (*i.e.* environmental domains or vegetation classes) a nominated number of times or quantitatively with a nominated proportion of total area (Margules *et al.* 1988). In this chapter, an iterative minimum set algorithm is run using a conservation-planning tool called

C-Plan. C-Plan (version 2.2 NSW NPWS 1999) was developed by the New South Wales National Parks and Wildlife Service (NSW NPWS) and has been used to select conservation sites in many parts of Australia (Pressey *et al.* 1996, Pressey 1999), South Africa (Lombard *et al.* 1997, Cowling 1999), and Canada (Forsyth *et. al,* pers. com). C-Plan runs as an extension of ArcView 3.1 and outputs of C-Plan are displayed as "views" in ArcView. Users of C-Plan have to build the necessary algorithms from within C-Plan according to their specific selection criteria. In the case of this study, an algorithm was written to select sites based on the highest summed irreplaceability values for environmental domain classification and vegetation classes.

4.1.3.2 Conservation Targets

Many international conservation organisations have advocated at least 10-12% of the total land area in each nation should be protected. The debate over whether these targets are useful is summarised by Soule and Sanjayan (1998). On the one hand, a target is a clear goal against which achievement can be assessed. Uniform targets are probably necessary if nations are to agree on biodiversity objectives and make progress towards them. On the other hand, it should also be remembered that any specific target for an area or proportion of an ecosystem to be protected is an essentially arbitrary choice, guided loosely, rather than defined, by science and usually reflecting political expediency. In the case of Guyana, the Government of Guyana has stated that it would like to conserve approximately 15 % of its land mass in a protected area network (Government of Guyana 1994). Thus, for the purposes of this study a conservation target of 15 % was applied.

4.2 METHODS

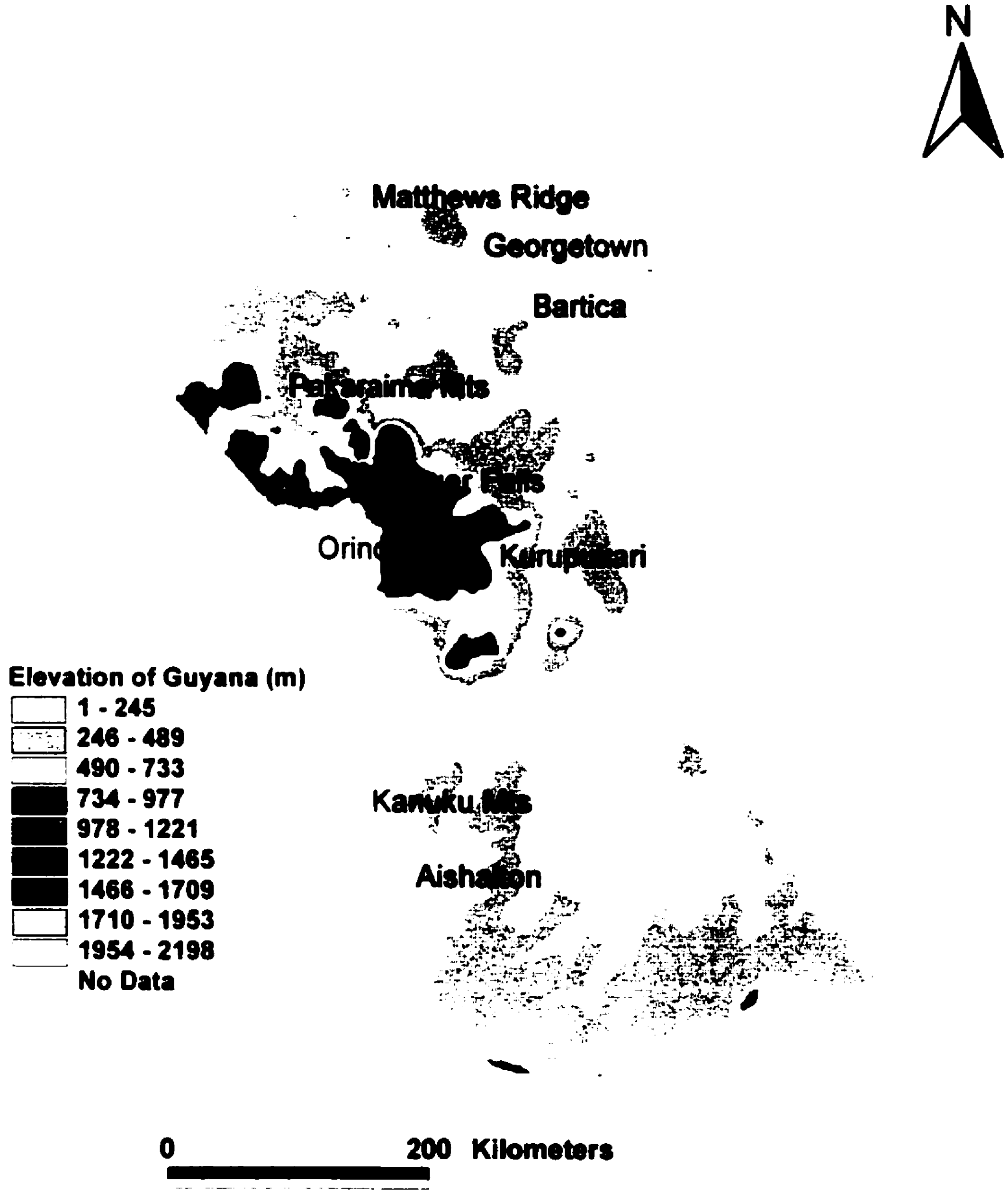
For the purposes of this study, the abiotic environmental variables used were climate, topography, and lithology. These variables were the only ones deemed to be accurate and readily available for Guyana. Although a soil map has been published (UNDP 1964), it is incomplete and at a very coarse scale. Two kinds of data were used in these analyses: continuous data, such as rainfall, temperature and topography; and categorical data such as lithology and vegetation classes. In the case of lithology, an attempt to convert categorical data into continuous data was made by scoring lithology types into soil fertility categories based on the classification of soil types by Ter Steege (1998). Although data were available for a 1 km^2 grid, the classification of environmental domains at a 1 km^2 grid size was computionally impossible. Data were therefore scaled up and used for a 4 km x 4 km (16 km^2) grid (13,751 grid cells in Guyana).

4.2.1 Data Collection

4.2.1.1 Digital Elevation Model (topography)

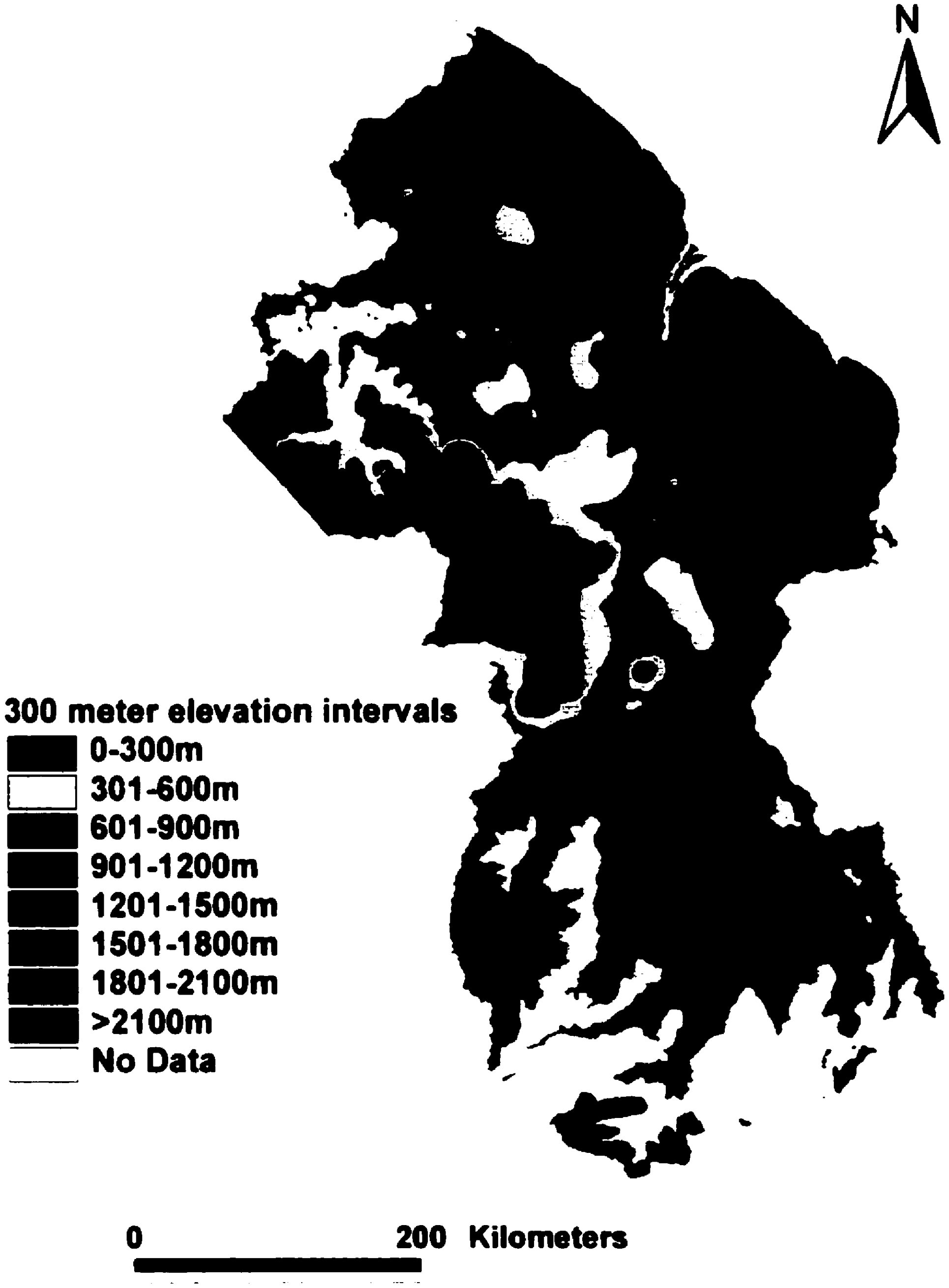
A digital elevation model (DEM) was refined and corrected from an existing DEM produced by the United States Geological Survey (USGS 1996) at a scale of 1:1,000,000, a grid size of approximately 1 km^2 (Figure 8). The DEM, at a resolution of 0.01 degree resulted in 247, 991 grid cells across Guyana. Digitised streams and rivers and spot heights were used to correct drainage basins using ANUDEM (Hutchinson 1989), a FORTRAN 77 program which interpolates elevation data onto a regular grid using a finite-difference method. The rivers and streams were digitised from the 1:100,000 topographical maps of Guyana using ARC/INFO (Figure 4, chapter 2). Parts of Guyana, most notably Georgetown, lie just below the sea level, however for the purposes of this study, areas below the sea level were considered to be at 0m. For the purposes of classifying environmental domains, elevation was divided up into 300m zones from 0 to 2198m (8 zones) (Figure 9). An index of terrain ruggedness was derived as the extent of variation of the target cell and the 8 surrounding cells (Figure 10). For the classification of environmental domains, a digital elevation model was derived for a 4 km x 4 km (16 km^2) grid (PATN is not capable of classifying all of the 1 km^2 grid cells simultaneously). The 16 km^2 DEM was derived by iteratively adding up grid cells in a 2 x 2 matrix and assigning the mean value of the four grid cells.

Figure 8: Elevation of Guyana



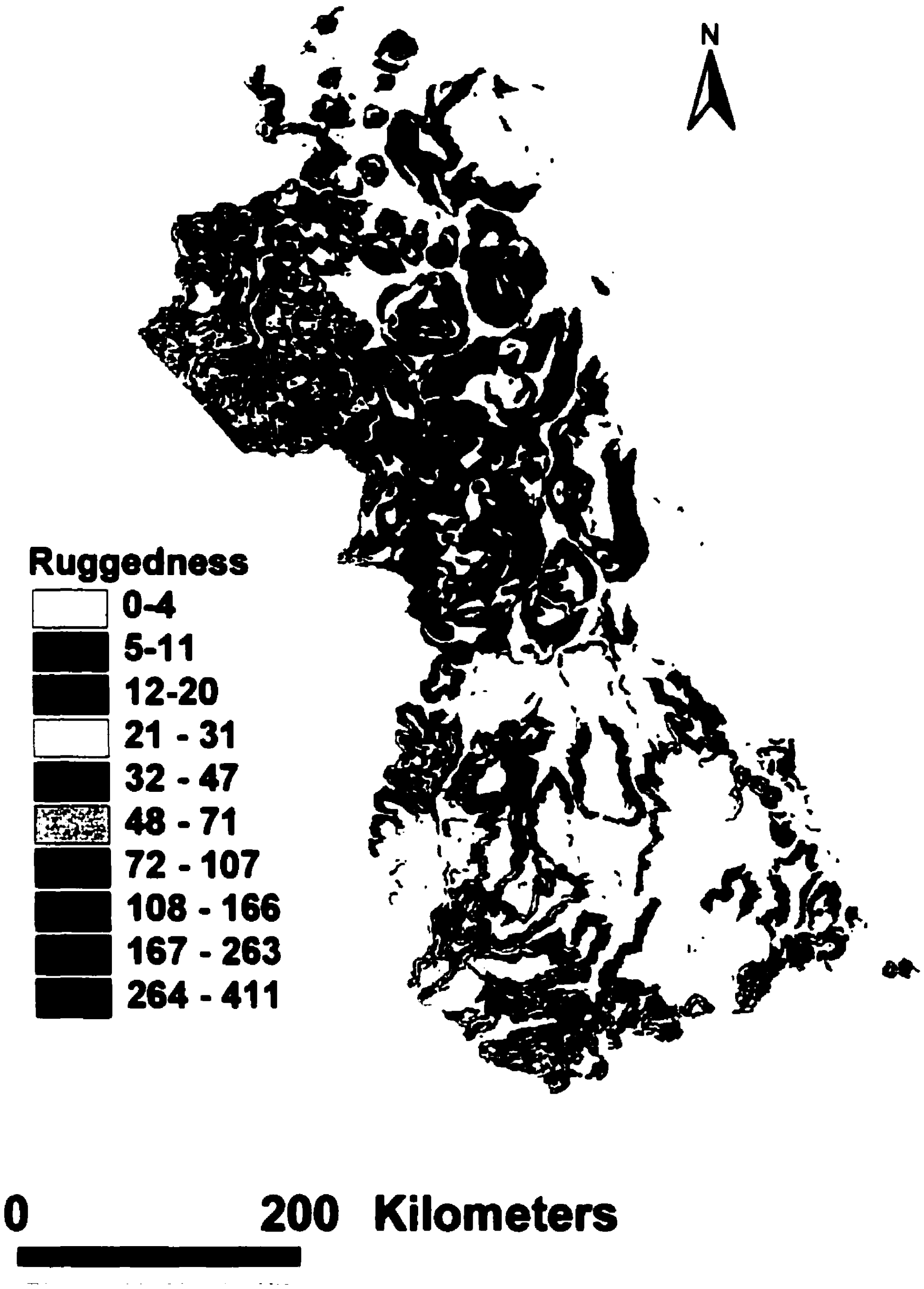
Source: US Geological Survey 1996

Figure 9: Elevation in 300m Intervals



Source: US Geological Survey 1996

Figure 10: Terrain Ruggedness



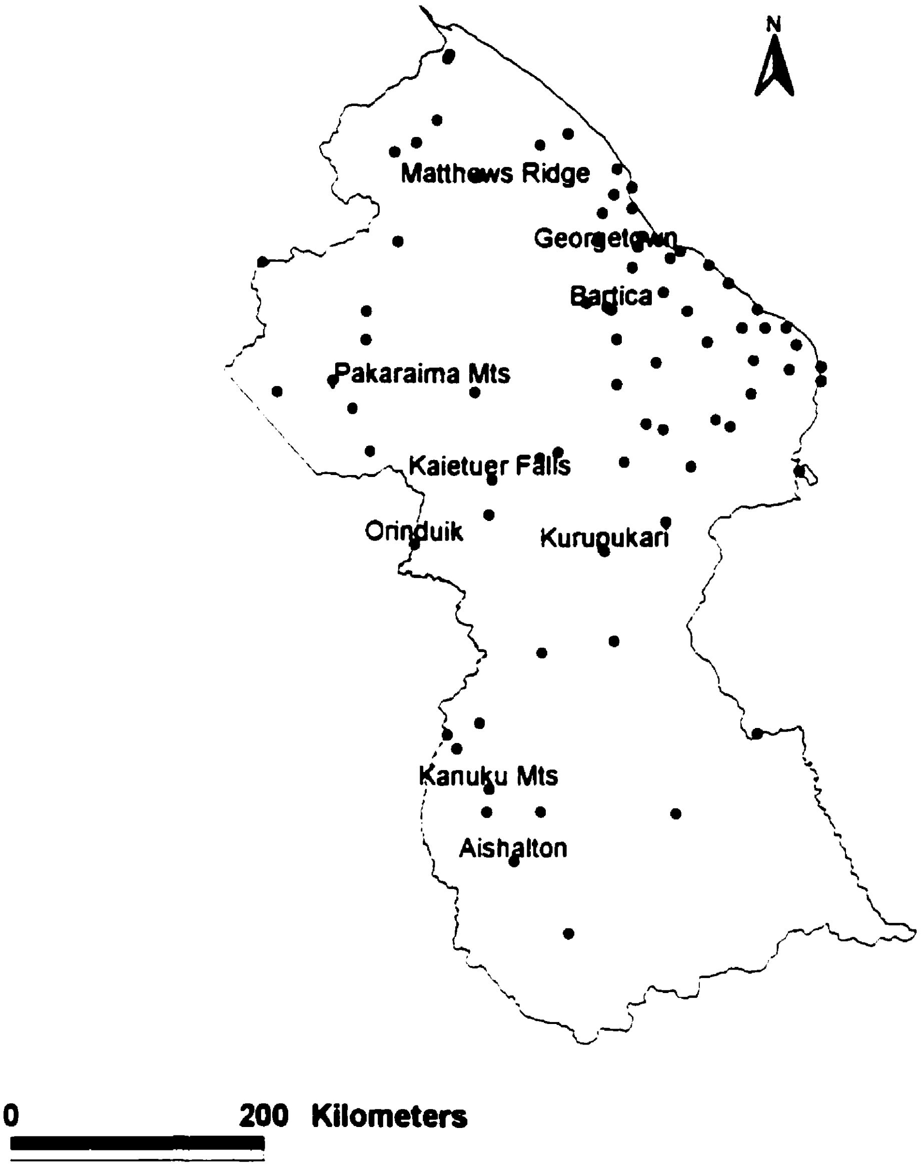
Source: U.S. Geological Survey 1996

4.2.1.2 Climate Records

Temperature and rainfall data were taken primarily from the Hydrometeorological Service of Guyana records, which recorded weather data from 234 stations over 20 years in Guyana. These data were also compared and where necessary complemented with data collected by the Centre for Resource and Environmental Studies (CRES) in Australia, which compiled the rainfall and temperature data for a Commonwealth-funded project that used meteorological information on Guyana. CRES based their meteorological data on data collected by the Consultative Group on International Agricultural Research (CGIAR).

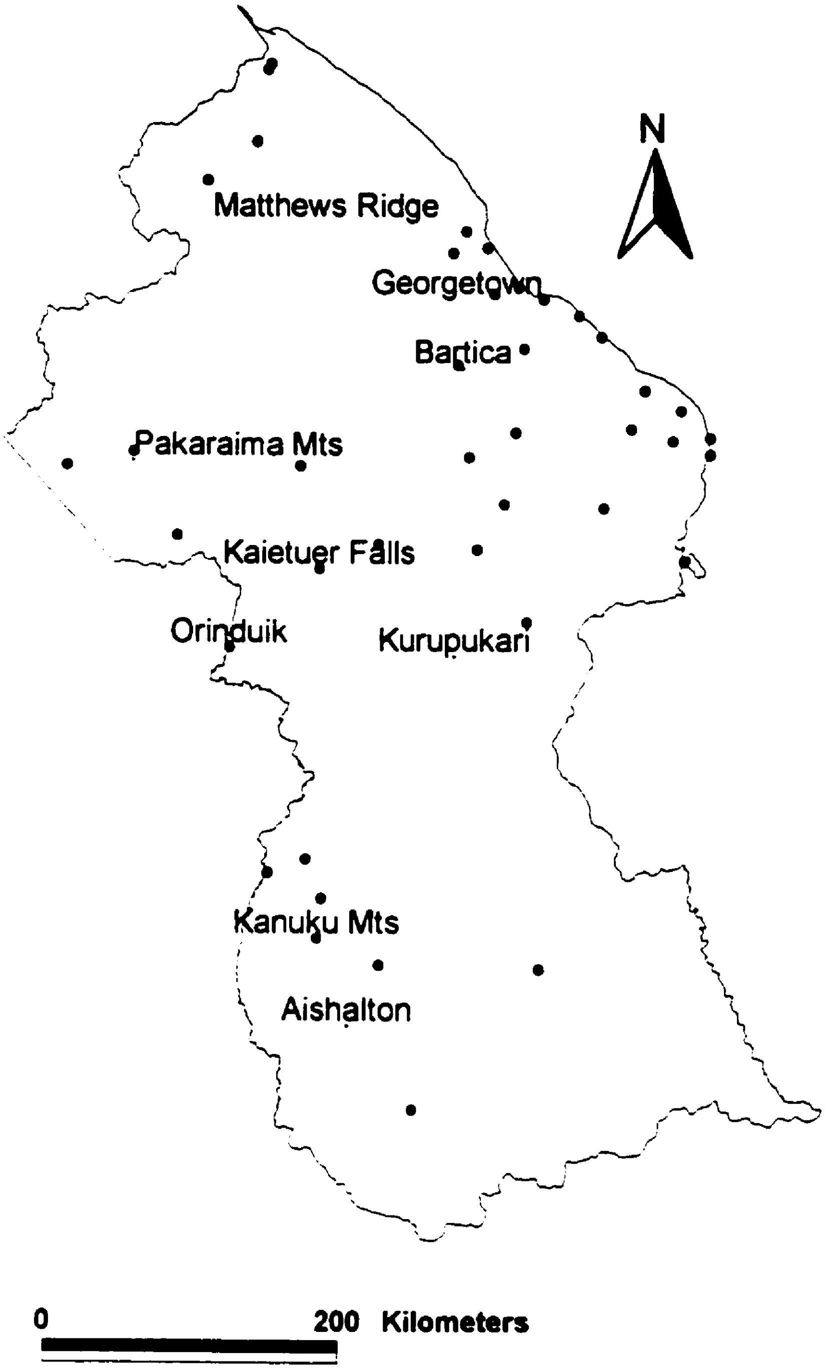
Average monthly rainfall data for 72 weather stations over 16 years (1972-1988) were entered into a database. The 72 stations were chosen from the 234 countrywide stations based on two criteria: a) uninterrupted rainfall data for at least 10 years; and b) accurate knowledge (preferably geocoded) of the station's location. See Figure 11 for locations of stations. Average minimum and maximum monthly temperatures for 45 weather stations over 14 years (1972-1986) were also entered into a database. The stations for temperature data were selected using the same conditions as for rainfall (see Figure 12 for location of temperature stations). The station values were uniformly weighted. Estimates of true error, averaged over the data points used, were less than 105 mm for rainfall and 0.5° C for temperature for every month of the year. Between 1988-1992, the climatic data for Guyana becomes patchy and unpredictable. More recently, the Hydrometeorological Service of Guyana has collected data for the period of 1992-1997 for a limited number of weather stations, however these data are not yet available.

Figure 11: Rainfall Stations across Guyana



Source: Hydrometeorological Service of Guyana. 1992

Figure 12: Temperature Stations across Guyana



Source: Hydrometeorological Service
of Guyana. 1992

4.2.1.3 Temperature and Rainfall Measurements

Monthly mean climate data for temperature and rainfall were spatially interpolated for the entire area of Guyana using ANUSPLIN (Hutchinson 1993), a program which calculates climate surfaces from individual points from which the longitude, latitude and elevation is known. The climatic surfaces were then fitted to the DEM to produce regular grids of monthly mean climate at the same spatial resolution of the DEM (approximately 1 km^2). The degree of data smoothing imposed by each fitted surface was chosen to minimise the predictive error of the surface by generalised cross validation (GCV) (Hutchinson 1993). The GCV was calculated by excluding each data point, in turn, and evaluating the degree to which that value was estimated by the remaining data.

Seven other climatic variables were derived using ANUCLIM (Version 1.8, Hutchinson 1998):

a) Maximum temperature of the warmest period;
b) Minimum temperature of the coldest period;
c) Temperature annual range (a-b);
d) Precipitation of the wettest period;
e) Precipitation of the driest period;
f) Precipitation seasonality (coefficient of variation); and
g) Precipitation of the driest month (October).

ANUCLIM is a program that can produce a set of estimates of climatic variables at any specific latitude, longitude and elevation based upon fitted surfaces of precipitation, and monthly mean maximum and minimum temperature from known meteorological data. The climate data for 16 km^2 grid was derived by iteratively adding up grid cells in a 2 x 2 matrix and assigning the mean value of the four grid cells in ArcView (version 3.1, ESRI 1998). The minimum, maximum, mean and standard deviation were calculated for each climatic layer in ArcView.

4.2.1.4. Lithology and Soil Fertility

The lithology map was digitised from the British Geological Survey Geology Map of Guyana produced in 1964 and updated by the Guyana Geology and Mines Commission in 1987 (Waldron 1987) (Figure 5, chapter 2). A soil map (UNDP 1964) was reclassified into three of soil fertility based on Ter Steege (1998) as follows (Figure 13):

a) low fertility (1)
b) intermediate fertility (2)
c) high fertility (3)

4.2.1.5 Vegetation

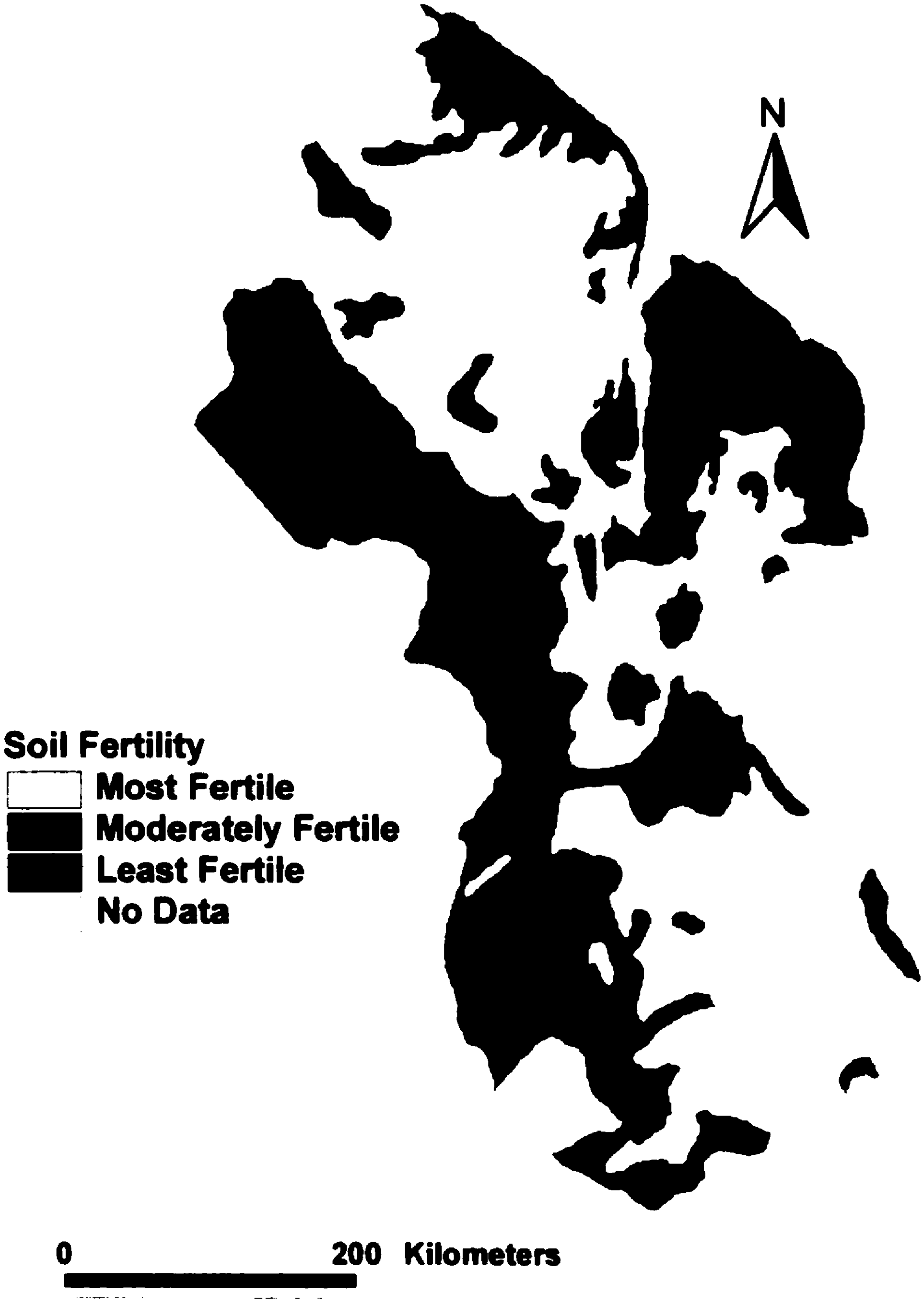
As described in chapter two, the vegetation map of Guyana was digitised from the vegetation map produced by the Smithsonian Institution's Biological Diversity of the Guianas Program based on LANDSAT TM images taken between 1990-1995 (Huber *et al.* 1995) (Figure 6, chapter 2).

4.2.2. Environmental Domain Classification

The various climate surfaces, lithology classifications, vegetation classes and the terrain classifications were used in a non-hierarchical clustering procedure (ALOC from the program PATN (Belbin 1993b)) to derive environmental domains following Belbin (1987, 1992) and Hutchinson *et al.* (1996). The procedure uses the Gower metric, to nominate classifications (BioRap Consortium 1996). There are four phases in this procedure:

a) All sites are allocated to their closest seed point (a seed point is defined as the data from the first row of any dataset).

Figure 13: Soil Fertility of Guyana



Source: UNDP 1964

b) The user defines how many groups the data should be classified into and based on this number a "maximum-allocation-radius" is determined. If the distance (Gower metric) between any object and its closest seed is greater than a user-specified value, the object forms a new group.

c) The centroids of all groups are calculated from the composition of the members of the groups.

d) Finally, the last phase removes an object from its group, recalculated the centroid of the group, determines the closest group centroid and allocates the object to the closest group. If the object changes groups, this is considered a re-allocation.

The procedure stops if after a complete pass of all objects, the number of re-allocations is less than or equal to the minimum number of re-allocations possible. The output was then exported into Idrisi (version 2.0 Clark University 1997) and examined. The output generated by ALOC was then submitted to a hierarchical classification using the FUSE program in the PATN program and the pattern of relationship between the domains was examined with a dendogram using the DEND module of PATN. A distance matrix was constructed in which the distance between each pair of sites was measured as the ultrametric distance between the domains of these sites, based on the hierarchical classification (Belbin 1993b).

A preliminary analysis of the climate variables generated by ANUCLIM to be used in the environmental domain classification showed that many of the variables were autocorrelated. Principal Component Analysis (Statistica 1999) was used to select those variables that best explained the data. These included average annual rainfall, average annual temperature, and precipitation of the driest period. In addition to these climatic variables, lithology, soil fertility, elevation by 300m and an index of ruggedness were used to classify domains. The variables were grouped into three categories: climate, terrain and substrate, each category contributing the same weight in the clustering.

The number of groups a user defines for domain classification is somewhat arbitrary, and the classification can be stopped at any level of division. However, one approach to determine how many domains are needed is to side step the traditional approach of classifying the data into an arbitrary number of environmental domains and ask how many domains-types could be represented in any 15 % of Guyana. Given the hierarchical nature of the clustering analysis, this can be determined and in the case of Guyana, it turns out to be 228 domains. Two other numbers of groups were chosen for comparison; 100 groups and 34 groups. One hundred groups were chosen arbitrarily for comparison, and thirty-four groups represents the number of vegetation classes identified in Guyana (Huber *et al.* 1995) and were used so that a comparison could be made with vegetation classes.

4.2.3 Irreplaceability

C-Plan (NSW NPWS 1999), was used to calculate irreplaceability values and select priority biodiversity sites. A uniform target of 15 % was used across Guyana in the case of environmental domains and vegetation classes. This was compared with a uniform target of 3 occurrences of each domain or vegetation type that is typically used with species data. The different targets were used to examine the outcome of sites using different representation targets and to compare sites selected using environmental domains and vegetation classes with the species data in later chapters.

The derived environmental domains were fitted to the 16 km^2 regular grid maps in ArcView and the amount of each environmental domain in each grid cell was calculated using "Tabulate Area" in the Spatial Analysis (version 1.1 ESRI 1998) extension of ArcView. The output from Tabulate Area as then used to build a C-Plan data matrix with the portion of each environmental domain found in each grid cell (13, 751 possible cells in total).

C-Plan calculates the "irreplaceability" value of each feature (domain or vegetation class) in the grid cell. A map of the "summed irreplaceability", or the sum of the irreplaceabilities of a grid cell, estimated separately for each of the environmental domains/vegetation classes it contains was produced and examined. Maps of summed irreplaceability values were compared for 34 environmental domains, 100 environmental domains, 228 environmental domains and vegetation classes. The correlation of the summed irreplaceability values between the 4 types of classifications was compared using Spearman rank order correlations.

4.2.4 Priority Biodiversity Site Selection

Priority biodiversity sites were selected using the summed irreplaceability values calculated for environmental domains and vegetation classes. Two targets were applied: 1) a 15 % representation of each domain/vegetation type; and 2) capturing 3 occurrences of each domain/vegetation type. A minimum set algorithm, designed from within the C-Plan program, was used to select priority sites based on their summed irreplaceability values. Sites with the highest summed irreplaceability value were selected first (Rule #1) until all features were represented at their target level. In the case of a tie, the grid cell closest to a grid cell already selected was chosen (Rule #2). Sites were selected based on their summed irreplaceability value, which took into consideration the "complementarity" to features preciously selected. The priority sites selected were those with the highest number of domains or vegetation classes previously not selected or in other words those with the high complementarity relative to other members of the selected set. The total number of grid cells required to meet a 15 % target was recorded and the rank order of the grid cell for each minimum sets was compared. The percent of overlap between minimum set selected for each of the four classifications was calculated using the Jaccard coefficient [number of sites shared/(number of additional grid cells for group A + number of additional grid cells for group B)] x 100 (after Van Jaarsveld *et al.* 1998). The minimum sets of priority sites reflect how different surrogate measures of biodiversity (in this case different classifications of domains and vegetation classes) prioritise sites for protection. Ideally, if the different surrogate measures of biodiversity represent the same elements of biodiversity, the overlap in locations using the different surrogates should be perfect or very high.

Lastly, to test the efficiency of each of the classifications as a surrogate for the other three classifications, feature accumulation curves were derived. A minimum set was run to select grid cells using the highest summed irreplaceability value for one of the classifications (e.g. 228 environmental domains) until all the features of that classification were satisfied. The percent of the target met was measured for each of the classifications and plotted against the number of sites selected. The feature accumulation curves for each classification were compared against a random curve generated using 1000 random runs. The areas under the curve were calculated for the each classification and the random curve. These curves were then compared. Confidence limits (97.5 % and 2.5 %) were derived using bootstrapping which ran 1000 replacement run for each combination. This was done for both a 15 % target and a target of 3 occurrences.

4.3 RESULTS

4.3.1 Climate

The climate data and maps presented here are the first attempt for Guyana to compile many sources of data over many years in a comprehensive manner. Data from the various weather stations were interpolated to produce the various maps

Figure 14: Mean Annual Temperature (C)

Source: Hydrometeorological Service
of Guyana. 1992

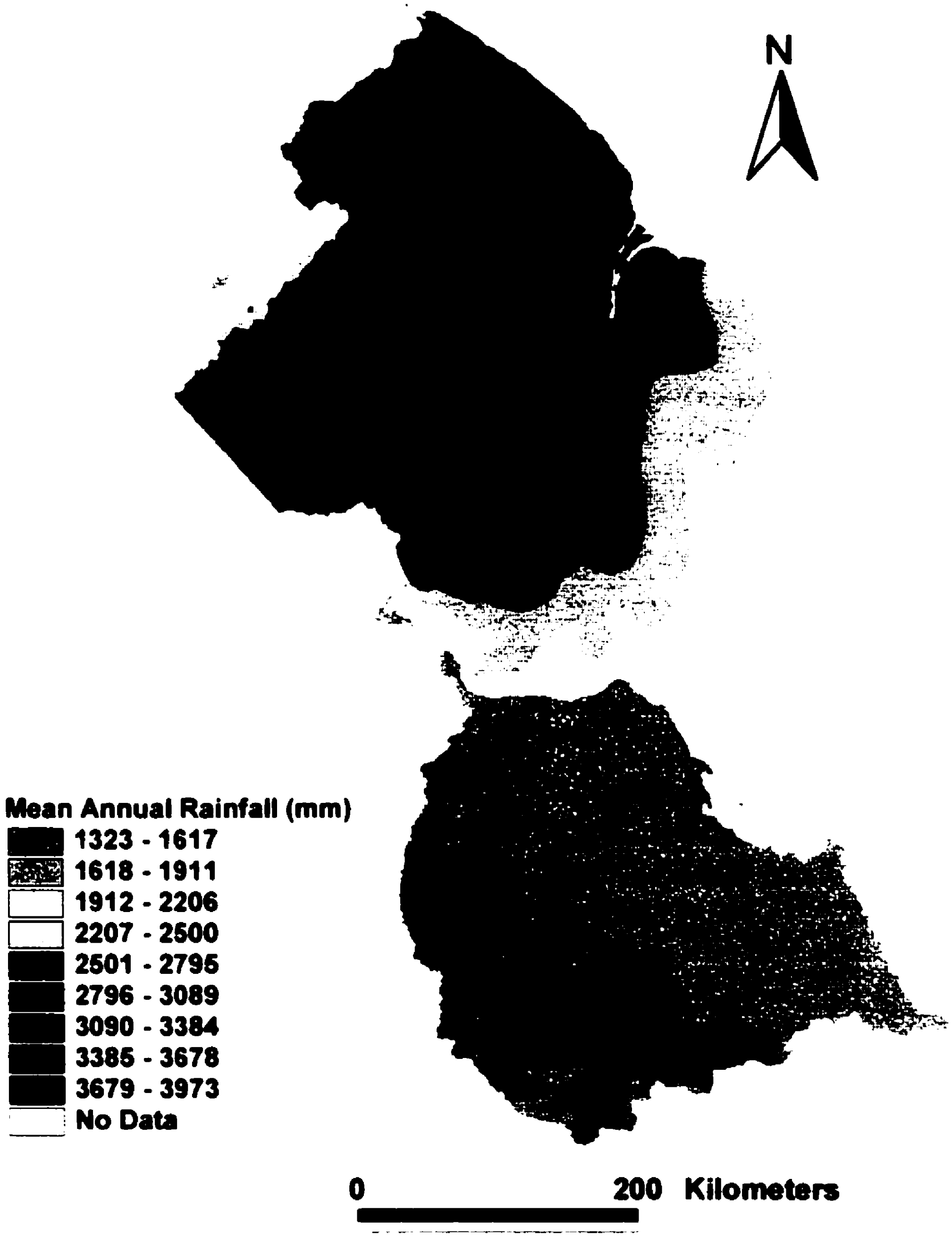
described below. Annual mean temperature varies from 14.0-28.1 °C (Table 3, Figure 14) with the coldest areas on top of Mt. Roraima and the peaks of the Pakaraima Mountains and the warmest areas in the savannas west of the Kanukus and in the southeast of the country.

The mean annual rainfall in Guyana ranges from 1323mm to 3973mm (Table 3, Figure 15).

Table 3 – Summary of Climatic Data

Climatic Variable (16 km^2 grid cell)	**Minimum**	**Mean**	**Maximum**	**Standard Deviation**
Annual mean Temperature (C°)	14.0	26.0	28.1	1.7
Maximum temperature of the warmest period (C°)	22.5	33.2	37.3	2.39
Minimum temperature of the coldest period (C°)	8.4	20.1	23.0	1.6
Temperature annual range (C°)	7.8	13.1	17.8	2.1
Annual mean Precipitation (mm)	1323	2438	3973	742.1
Precipitation of the wettest period (mm)	245	395	616	75.1
Precipitation of the driest period (mm)	0	111.5	268	48.7
Precipitation seasonality (CV)	30	59.9	117	20.4
Precipitation of the driest month (October)(mm)	0	77.48	211	52.78

Figure 15: Mean Annual Rainfall (mm)



Source: Hydrometeorological Service of Guyana. 1992

The north-east of the country receives the greatest amount of annual rainfall (3400-3973mm), in particular the area north of the Cuyuni River. This is followed by the area north of Kaietuer Falls where the Mazaruni River branches from the Essequibo river. The driest part of the country is the extreme south-west corner, to the west of the Kanuku Mountains (1323-1500mm) and along the border with Brazil. The driest month of the year is October where the rainfall varies from 0 to 211mm across the country (Table 3, Figure 16).

4.3.2 Topography

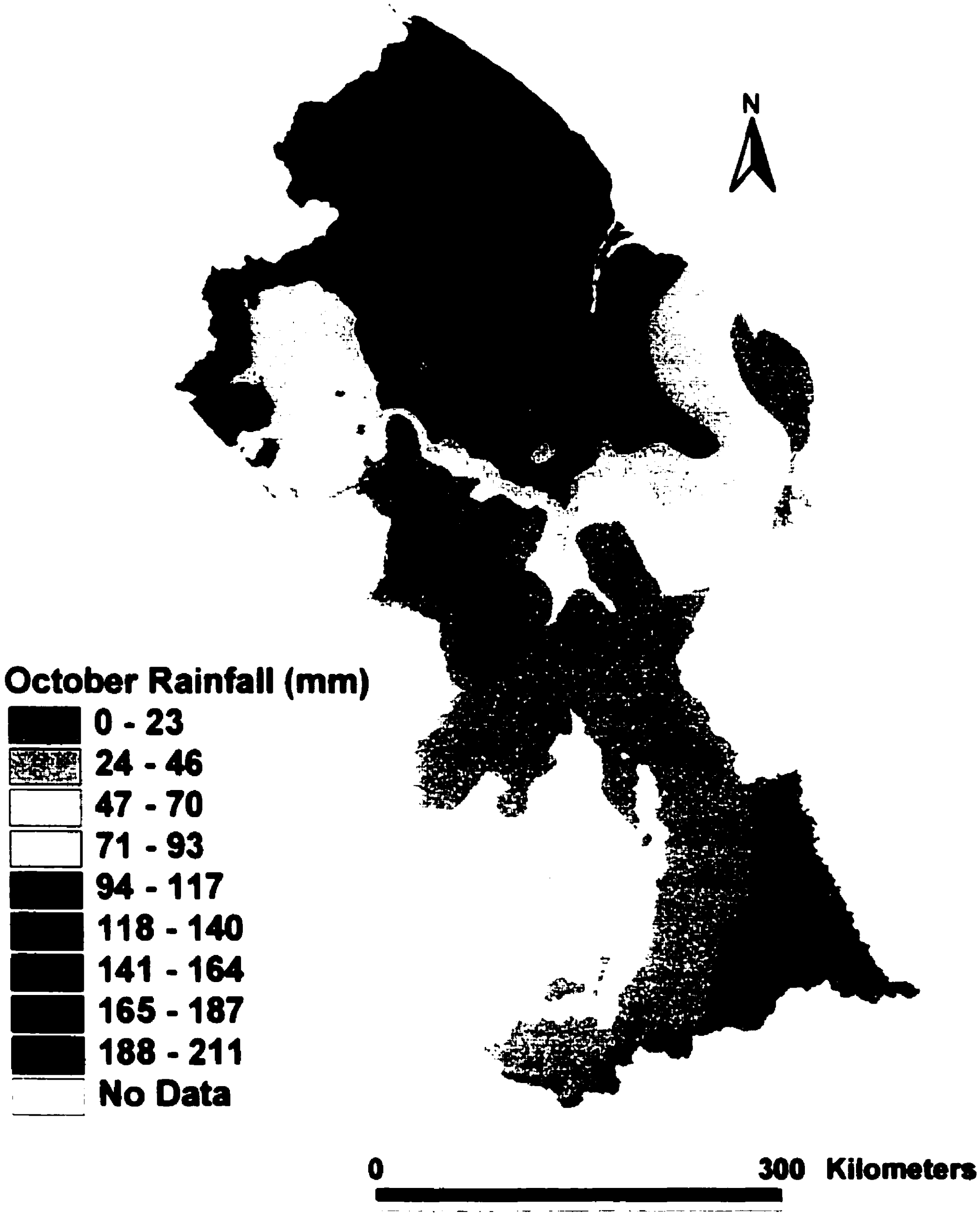
Elevation in Guyana ranges from 0m (or just below sea level in some parts of Georgetown) to 2198m at the highest part of Mt. Roraima that lies within the border of Guyana (Figure 8)(Mt. Roraima reaches 2,772m at its peak in Venezuela). The highest peaks are found in the Pakaraima Mountains and include Mt. Wokumung (2,134m) and Mt. Ayanganna (2,042m). Guyana is characterised by its central low lying forests bordered by the Pakaraima Mountains to the west and its relatively low lying savannas interspersed to the south-west by the Kanuku Mountains.

The index of ruggedness ranged from 0-411. The most rugged areas were found in the Pakaraima Mountains, north of Kaieteur and in the Kanuku Mountains (Figure 10).

4.3.3 Lithology, Geology and Soil Fertility

As discussed in chapter two, there are 14 types of parent material or lithology in Guyana (Figure 5, chapter 2). Each of these types was used to classify domains. In addition, the three categories of soil fertility (most fertile, moderately fertile and least fertile) (Figure 13) were used. The most fertile areas are found along the eastern coast, in the north-central part of the country, and in the south-eastern

Figure 16: Rainfall for October (mm)



Source: Hydrometeorological Service
of Guyana. 1992

corner. These areas correspond to the podzol (loamy) soils and the brown sand areas (UNDP 1964).

4.3.4 Vegetation

There are 34 different vegetation classes described by the vegetation map of Huber *et al.* (1995) (Figure 6, chapter 2). The predominant vegetation in Guyana is tall, evergreen non-flooded forest found primarily in the north-central part of the country followed by mora forests and lower montane sclerophyllous forests. The rarest vegetation type in Guyana is the high-tepui evergreen forest found from 2,000-2,700m. Forest types cover over 80% of the country, with open savannas and shrublands occurring mainly in the south of the country.

4.3.5 Environmental Domains

The three classifications of environmental domains (228, 100 and 34 groups) are presented in Figures 17 a-c. For all three classifications, the area covering Mt. Roraima constitutes a separate domain. The Pakaraima Mountains are divided into several domains in all three classifications, as is the central-north lowland forests. When the domain classification of 34 groups is compared with the vegetation map they show similar divisions of the north-east part of the country, the eastern parts of the country and the Pakaraima Mountains. However, more environmental domains are found throughout the north-central part of the country and the southeast part of the country, which has not been well studied botanically.

4.3.6 Irreplaceability

The summed irreplaceability values for the three environmental domain classifications and the vegetation map were calculated. The resulting maps of summed irreplaceability values are presented in Figures 18 a-h.

Figure 17a: 228 Environmental Domains

Figure 17b: 100 Environmental Domains

Figure 17c: 34 Environmental Domains

Figure 18a: Summed Irreplaceability for 228 Domains

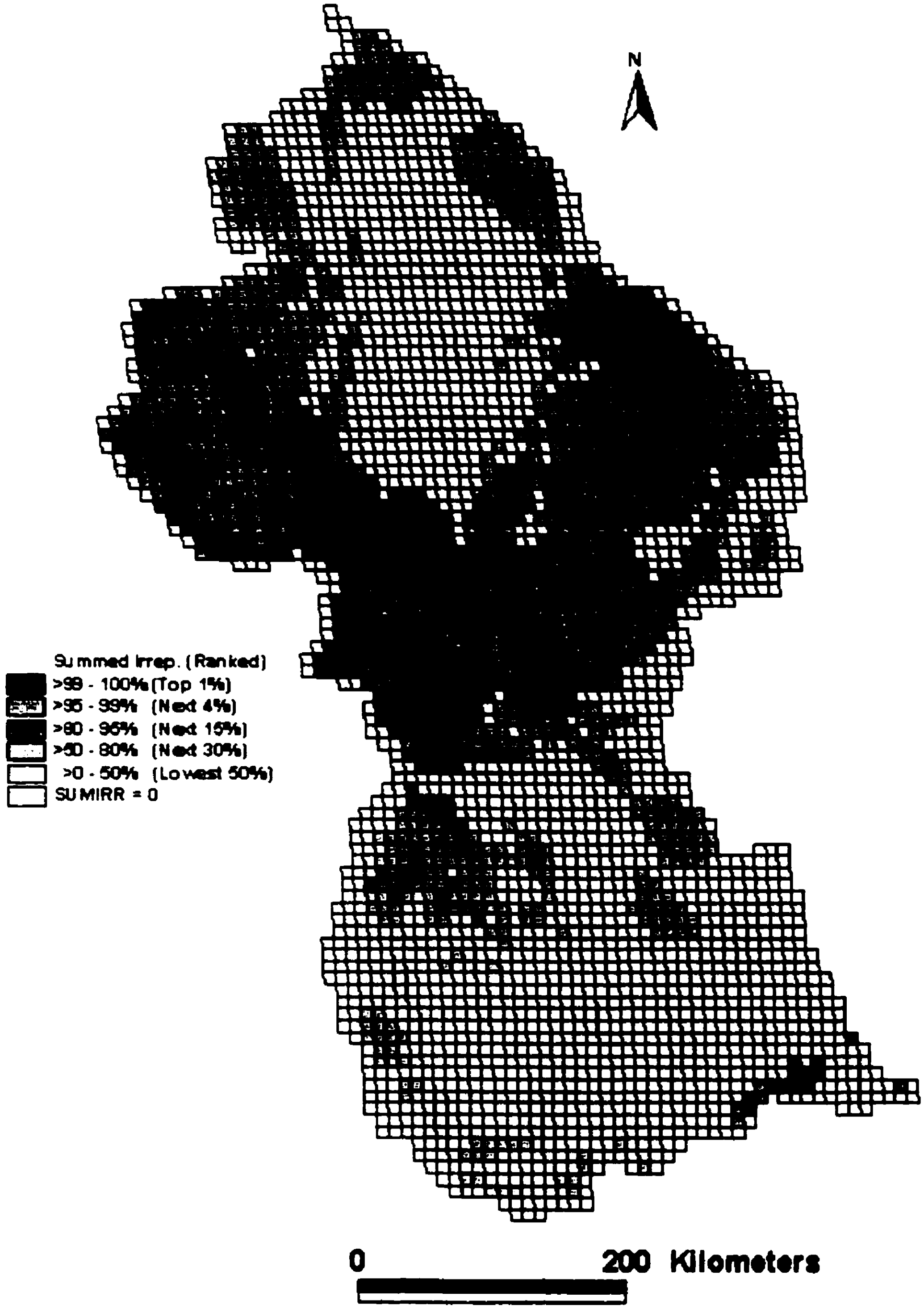


Figure 18b: Summed Irreplaceability for 100 Domains

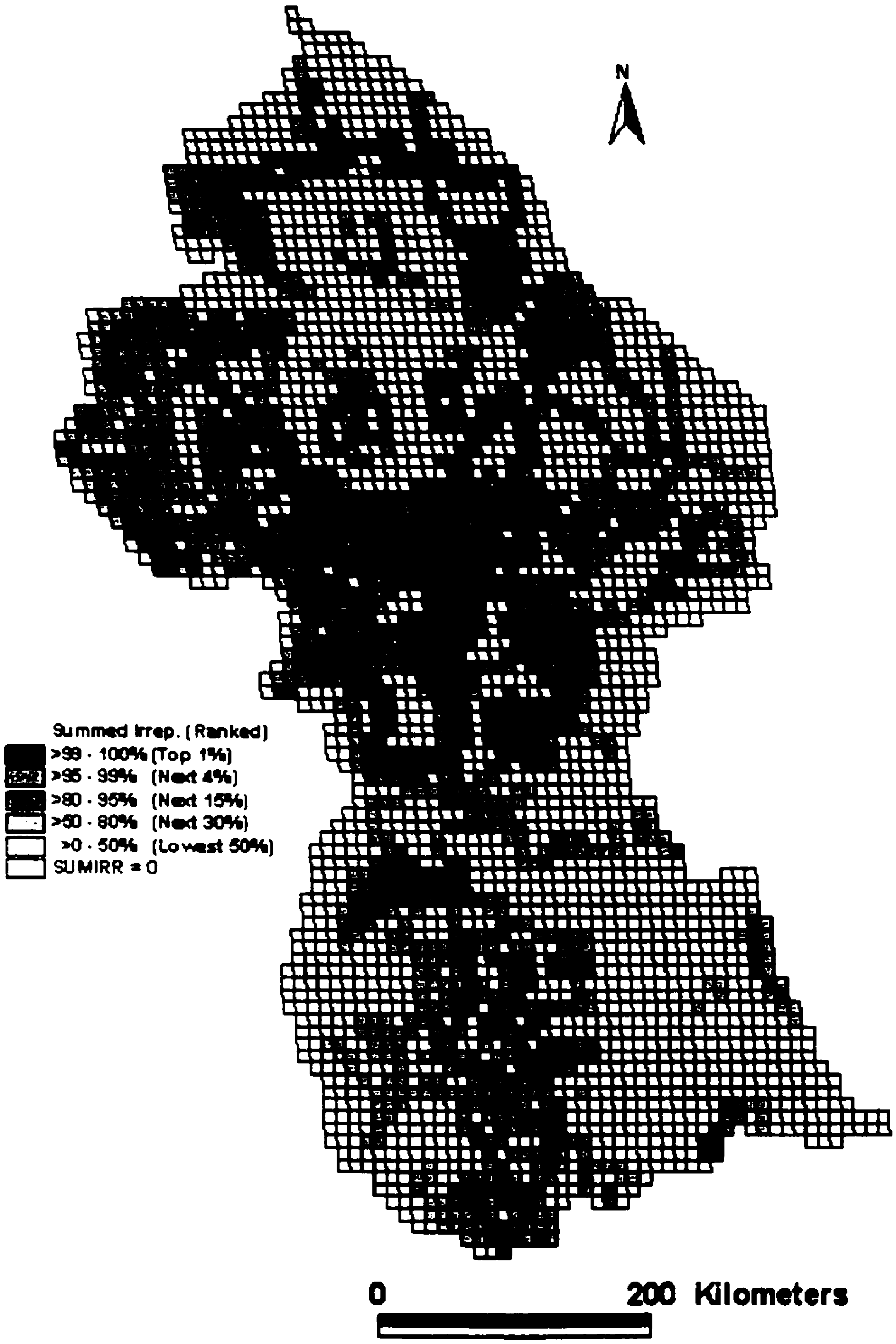


Figure 18c: Summed Irreplaceability for 34 Domains

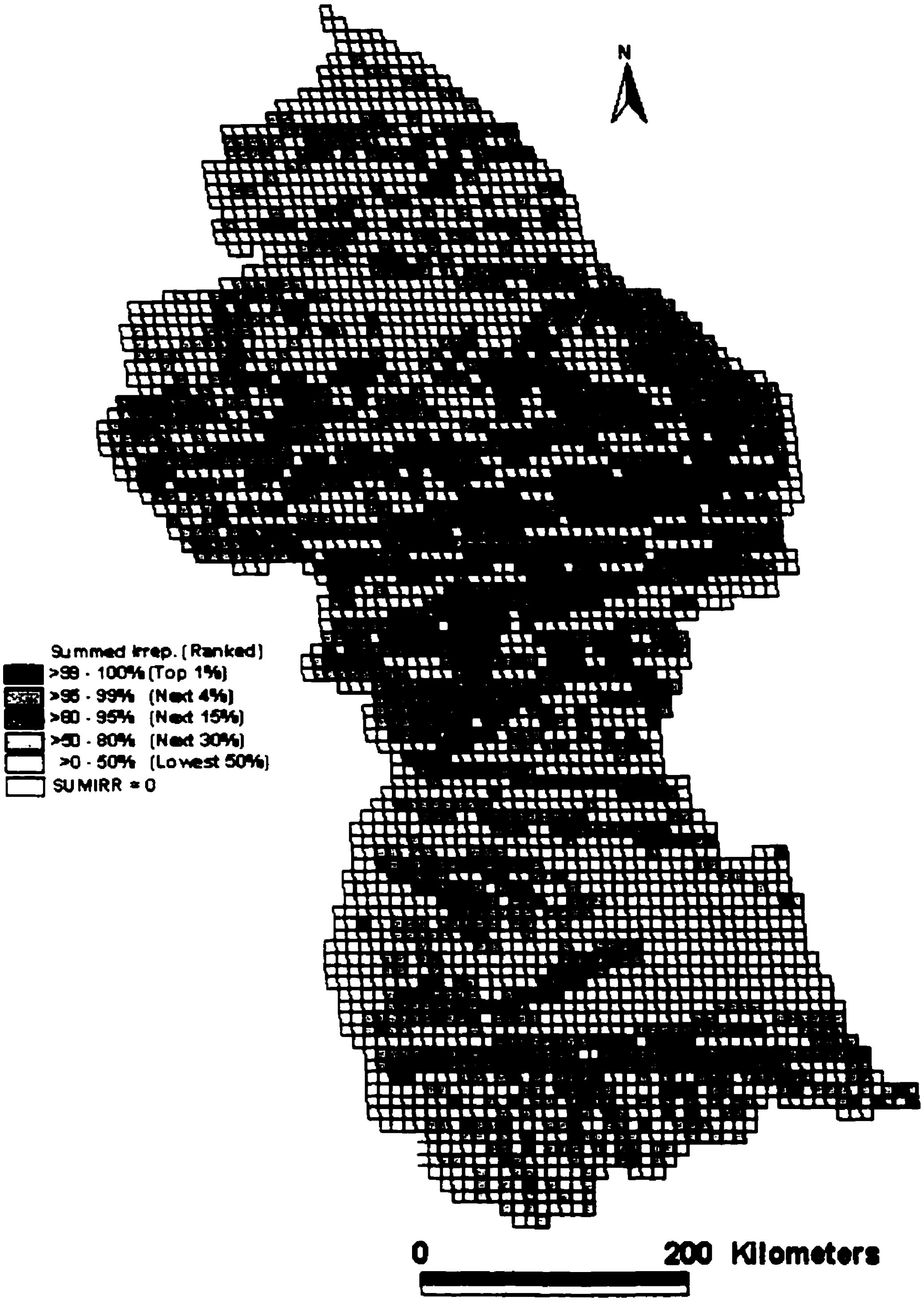
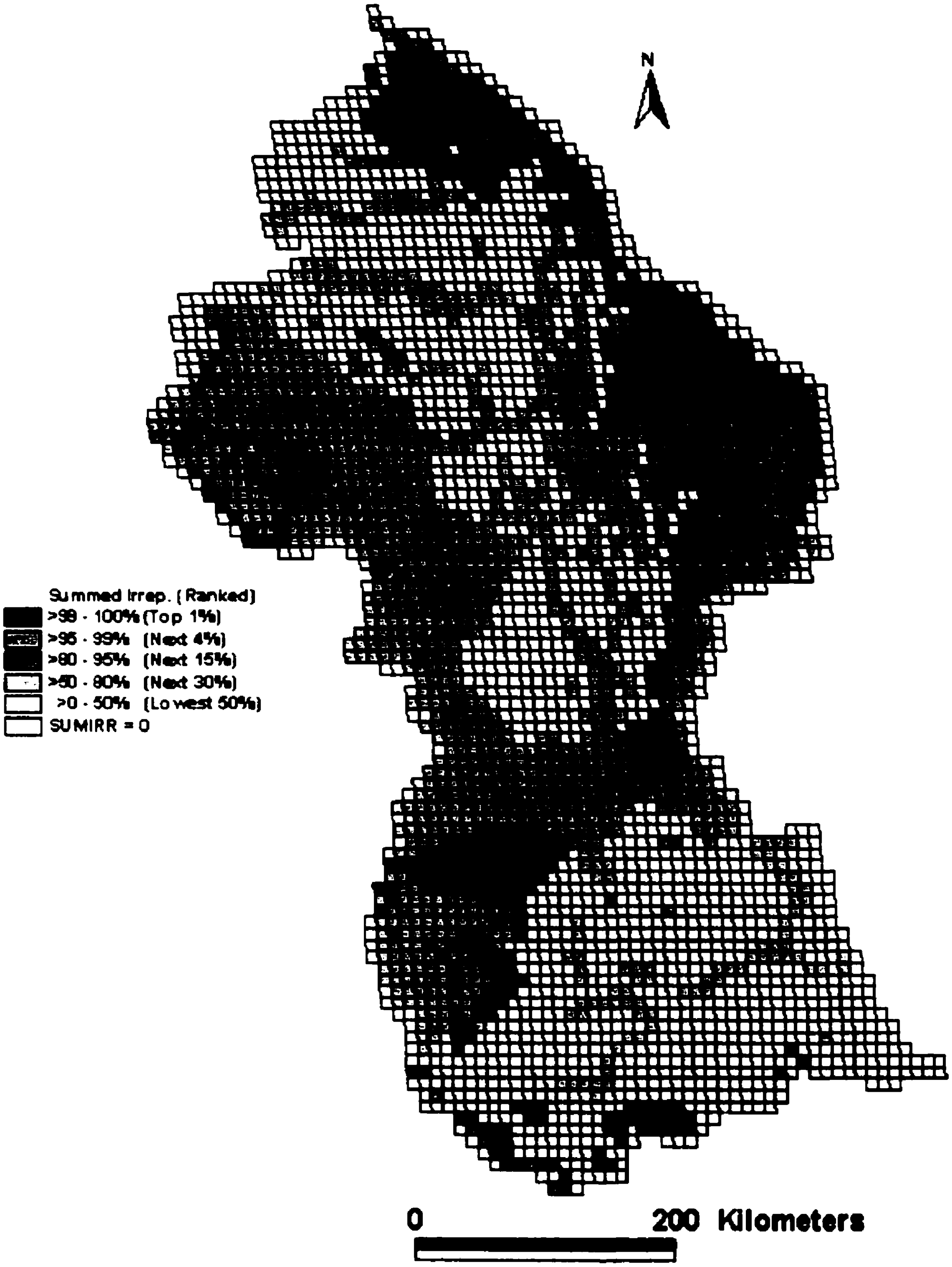


Figure 18d: Summed Irreplaceability for Vegetation Classes



Summed irreplaceability values represent the sum of the initial irreplaceability value for each feature before any sites are selected for protection. Thus, they represent an initial "snapshot" of the relative value of each grid cell. All eight resulting summed irreplaceability maps show the grid cells covering Mt. Roraima within the top 1% of the highest summed irreplaceability values. Other areas within upper 5 % common to all eight classifications include the central forests and Kanuku Mountains, however the exact grid cells in these sites appear to differ. The map of summed irreplaceability values derived for 228 environmental domains (615 grid cells required to represent all features at a target of 15 % and 646 grid cells required to represent each domain 3 times) shows the sites of highest summed irreplaceability to be in the north-west of the Pakaraima range near the Werushima range, the southern part of the Pakaraima range near Mt. Roraima and Mt. Ayanganna, the Potaro river basin, the western Kanuku Mountains and the south-east corner of the New River Triangle area. The map of summed irreplaceability values derived for 100 environmental domains (310 grid cells required to represent all features at a target of 15 % and 290 grid cells required for a target of 3 occurrences) shows the sites of highest summed irreplaceability to be more widely scattered throughout the northern half of the country, particularly in the central part of the country and to include the eastern Kanuku Mountains. The map of summed irreplaceability derived for 34 domains (291 grid cells required to represent all features at a target of 15 % and 98 grid cells required for a target of 3 occurrences) resembles the map for 100 domains, however the priority assigned to some cells is sometimes different, and there are fewer sites in the central part of the country that are in the upper 1 %. Finally, the map of summed irreplaceability values derived for vegetation classes (520 grid cell required to represent all features at a target of 15 % and 580 grid cells for a target of 3 occurrences) shows the Pakaraima Mountains, as well at Mt. Roraima and the Kanuku Mountains as being in the top 5 %, however the coastal area in the north-east is also valued in the top 5 %.

The initial summed irreplaceability values for each type of classification using a target of 15 % was compared using Spearman Rank correlations. There was a very weak, positive relationship between the 228 domain classification, the 100 environmental domain classification and 34 environmental domain classification (Table 4), and a very weak negative correlation between the 228, 100 and 34 environmental domains and vegetation classes (Table 4).

Table 4 – Spearman Rank Correlation of Summed Irreplaceability

Classification	Number of grid cells possible	Spearman R	p-level
228 env. domain x 100 env. domain	3402	0.223	0.0000
228 env. domain x 34 env. domain	3394	0.224	0.0000
228 env. domain x vegetation classes	3321	-0.170	0.0000
100 env domain x 34 env domain	3394	0.391	0.0000
100 env domains x Vegetation classes	3321	-0.899	0.0000
34 env domain x Vegetation classes	3321	-0.096	0.0000

4.3.7 Selection of Priority Biodiversity Sites

The selection of priority biodiversity sites was carried out using an iterative minimum set algorithm that selected the site with the highest summed irreplaceability value. The cell with the highest summed irreplaceability value was selected first and then the relative irreplaceability of each grid cell was re-calculated and the next highest cell was selected until all features were represented by 15 % of their distribution across Guyana or 3 occurrences. Maps of the minimum sets for both environmental domain classification and vegetation classes are presented in Figures 19 a- h for both targets.

The map of grid cells selected for 228 environmental domains showed a concentration of cells in the north-central part of the country and widely scattered cells across the country (Figure 19a and b). The grid cells selected seem to sample most of different areas of Guyana, with a concentration in the Pakaraima Mountains, the Potaro river basin, the Kanuku Mountains and along the western coast. The map of grid cells selected for 100 environmental domains shows a wide scatter of grid cells across the country in a somewhat uniform pattern with a slight concentration in the north-central part of the country (Figure 19c and d). The selected sites based on 34 environmental domains shows more clustering in the cells selected than for either the 228 or 100 domain classifications (Figure 19e and f). The clustering occurs along the north-west coast and into the Pakaraima Mountains. There are also clusters of cells in the south-east of the country and in the central-east. The grid cells selected based on vegetation type shows predominance for vegetation classes in central-north of the country, the Pakaraima Mountains and the southeast of the country (Figure 19g and h). The results of the minimum set selected using vegetation type indicate that there was very little difference in summed irreplaceability values for many of the grid cells and hence, adjacent cells were selected once the cell with the highest summed irreplaceability was selected (rule #2 of the algorithm). Rule # 2 was used in over 65% of the cell selection for vegetation classes, whereas it was used in less than 20 % of the grid cells selections for 228, 100 environmental domains and approximately 28 % of the cells selected for 34 environmental domains. The degree of overlap between selected sites using the four different classifications for a target of 15 % is compared in Table 5. A quarter of sites selected based on vegetation classes were also selected with the 34 environmental domain classification. The overlap of cells selected in a minimum set for all four classifications was 0.78 %.

Figure 19: (a) Minimum Set of Sites with 228 Domains 15 % Target;

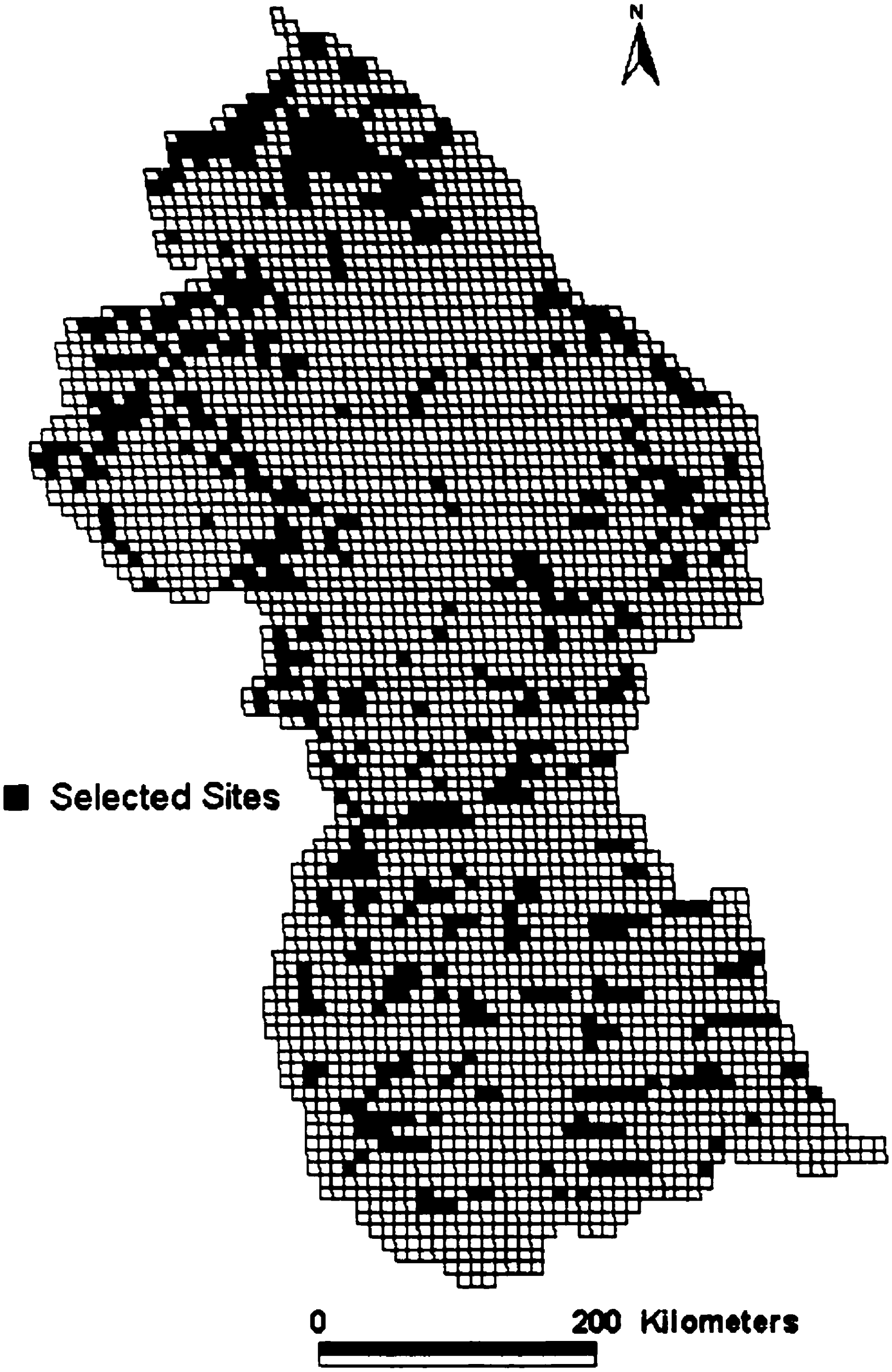


Figure 19: (b) Minimum Set of Sites with 228 Domains 3 Occurrences Target

Figure 19: (c) Minimum Set of Sites with 100 Domains 15 % Target;

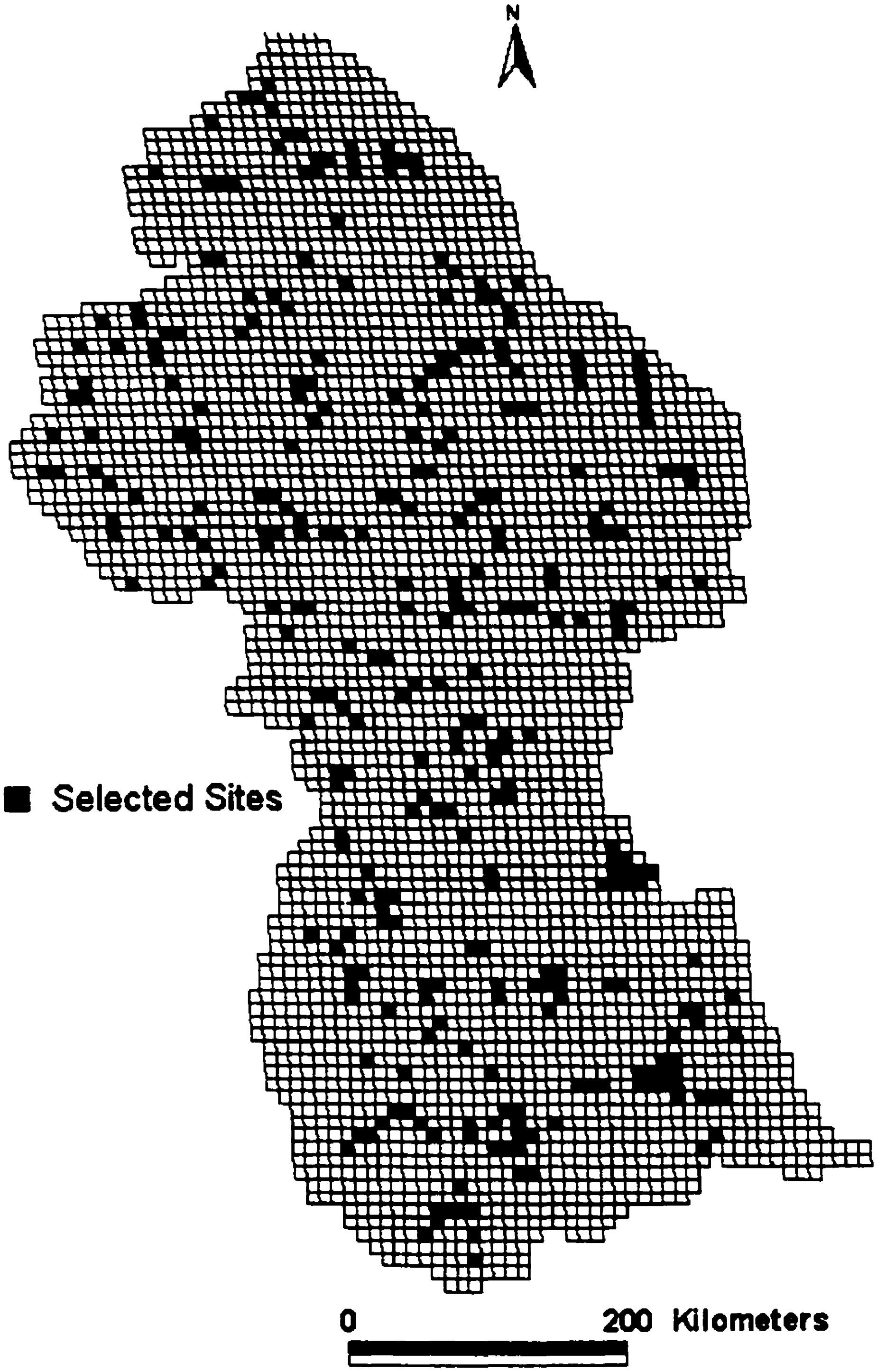


Figure 19: (d) Minimum Set of Sites with 100 Domains 3 Occurrences Target

Figure 19: (e) Minimum Set of Sites with 34 Domains 15 % Target;

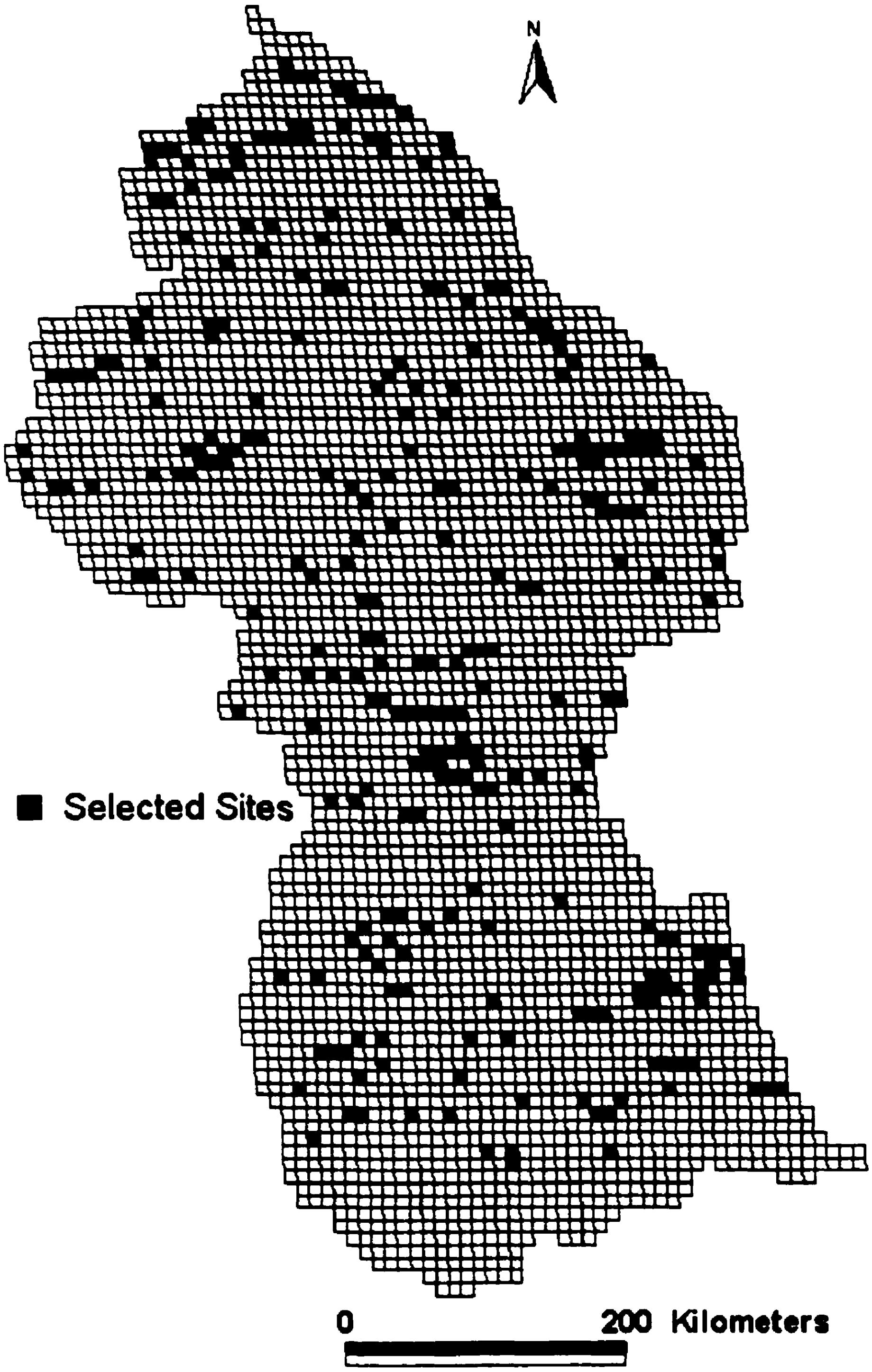


Figure 19: (f) Minimum Set of Sites with 34 Domains 3 Occurrences Target

Figure 19: (g) Minimum Set of Sites with Vegetation Classes 15 % Target;

Figure 19: (h) Minimum Set of Sites with Vegetation Classes 3 Occurrences Target

Table 5 - Comparison of Minimum Sets

Minimum Set Comparisons	**% Overlap**
228 domains x 100 domains	13.7
228 domains x 34 domains	23.4
228 domains x vegetation classes	15.3
228 domains x 100 domains x 34 domains	4.2
228 domains x 100 domains x vegetation classes	2.1
228 domains x 34 domains x vegetation classes	6.8
228 domains x 100 domains x 34 domains x vegetation classes	0.78
100 domains x 34 domains	10.5
100 domains x vegetation classes	9.2
100 domains x 34 domains x vegetation classes	2.0
34 domains x vegetation classes	18.9

4.3. 8 Difference in Targets

The overlap in sites selected using a 15 % target and a target of 3 occurrences was quite high (Table 6). The average overlap between the two targets was 90.1 %. A high percent of overlap is excepted as the same criterion of highest summed irreplaceability was being applied. A 15 % target appears to be the near equivalent of representing each feature in the classification 3 times.

Table 6 - Overlap in grid cells for minimum sets run using a target of 15 % and a target of 3 occurrences

Classification	**% overlap**
228 Domains	95 %
100 Domains	93.5 %
34 Domains	83 %
Vegetation Type	89 %

The feature accumulation curves are presented in Figures 20 a-d for a target of 15 %. The interpretation of the feature accumulation curves is done by examining the areas under the curve (Figures 21 (a-d)). The area under the curve is calculated for: a) the optimal – the best possible case where the classification in question is being used to select grid cells to capture all the necessary features; b) each surrogate – where the remaining classifications are used to select grid cells and the rate at which the features of the classification in question are accumulated is measured; and c) random – where a random selection of sites for each classifications is run (1000 times) and the area under the random curve is calculated.

The comparisons of areas under the feature accumulation curve for 228 domains shows the optimal (228 domains selecting 228 domains) is significantly better than any of the other classification in capturing the features of 228 environmental domains (Figure 21a). Vegetation classes are the next best surrogate for 228 environmental domains and do significantly better than random, however 100 domains and 34 domains do not perform any better than random (Figure 21a). For 100 environmental domains, the lower confidence limits of the optimal overlaps with the upper confidence limits of 100 environmental domains being selected by 228 domains slightly (Figure 21b). The confidence limits of vegetation classes as a surrogate for 100 domains also overlap with the limits of 228 domains as a surrogate. These two surrogates (228 domains and vegetation classes) capture the features of the 100 environmental domains better than random and significantly better than 34 environmental domains (Figure 21b). For the case of 34 domains, the optimal doesn't do better than 34 domains selected by vegetation classes and barely does better when 228 domains are used to select sites (Figure 21c). It does, however do better than random and when 100 environmental domains are used to select sites, it fails to pick up any of the 34 environmental domains. Finally, the optimal for vegetation classes is significantly better than using any of the other classification types (Figure 21d). The classification of 228 domains as a surrogate for vegetation classes does significantly better than random and than the two other classifications (Figure21 d).

4.4 DISCUSSION

Data on the environmental variables and vegetation classes of Guyana show that Guyana is a heavily forested country, with primarily low-lying forests and savannas. The two mountain ranges, the Pakaraima and Kanukus, influence the temperature range and rainfall range in the country. The naturally occurring savannas in the south of the country have, on average, the highest mean annual temperatures. The main forest types, tall, evergreen non-flooded and flooded forests are found on loamy-clay soils and brown sands over migmatite, and granitoids. These forests are primarily wet forests, receiving on average 3300-3800 mm of rainfall annually. The classification of environmental variables into domains attempts to represent this topographical, vegetative and climatic variation diversity.

Environmental domain classification and vegetation classes can both be considered 'coarse' filters of biodiversity information and surrogate measures of biodiversity. Their ability to represent the elements of biodiversity should be similar, and should be comparable with approaches based on the distribution of known species. Data presented in this chapter indicate that there are large differences in the location of priority biodiversity sites identified using vegetation classes and environmental domains.

Figure 20: (a) Feature Accumulation Curve 228 Domains; (b) Feature Accumulation Curve 100 Domains

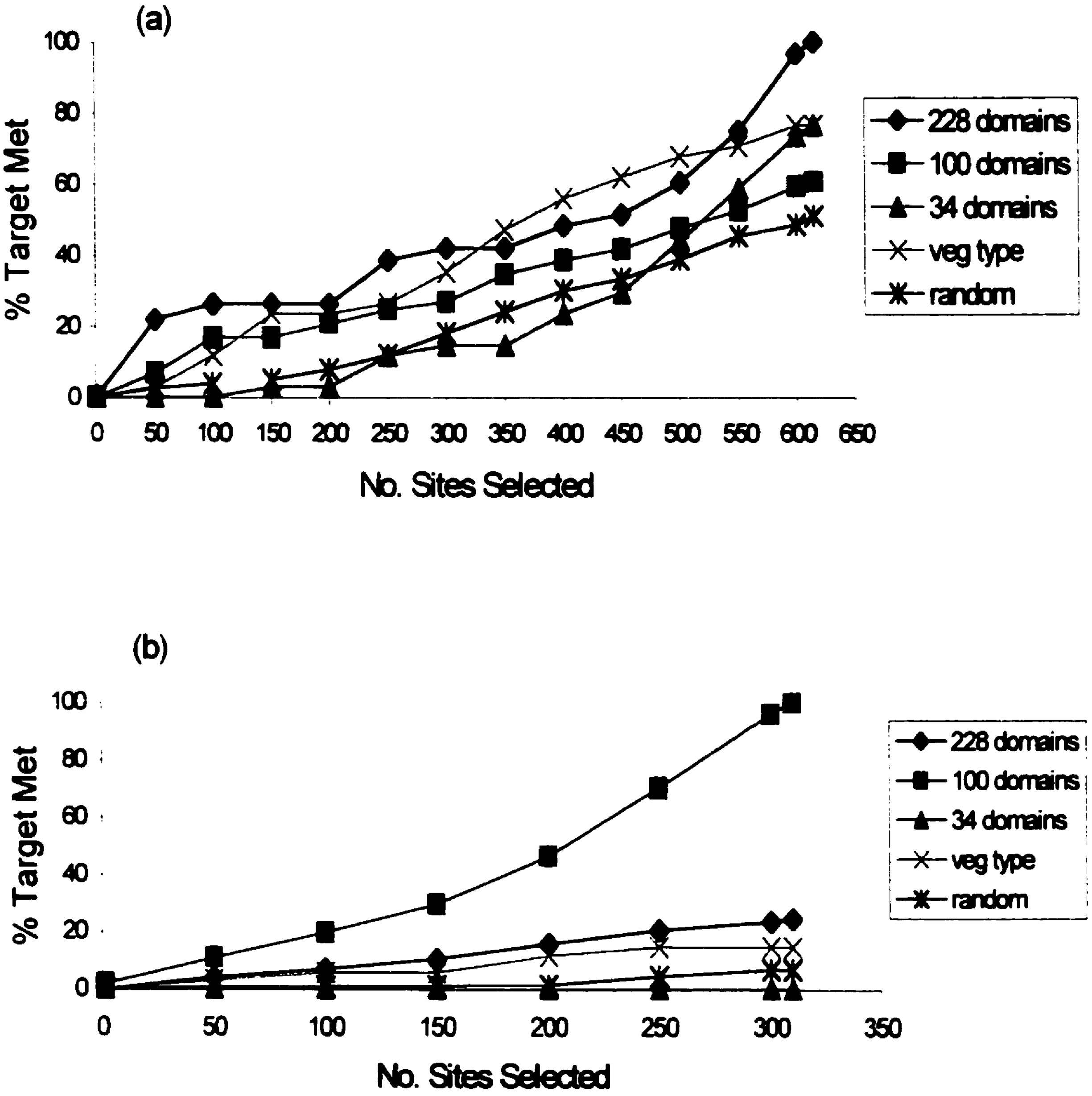


Figure 20: (c) Feature Accumulation Curve 34 Domains; (d) Feature Accumulation Curve Vegetation Classes

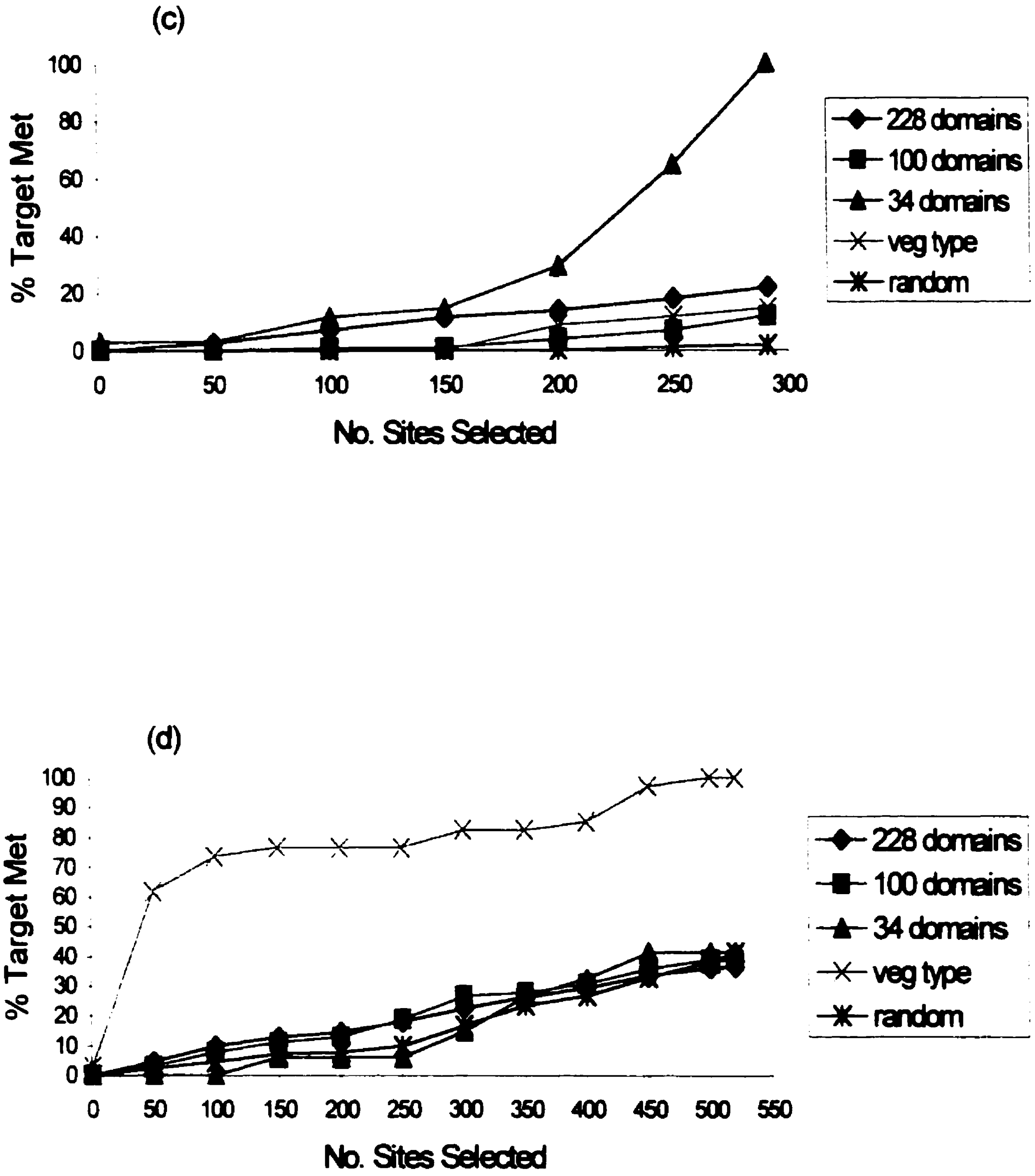


Figure 21: (a) Comparison of Areas 228 Domains; (b) Comparison of Areas 100 Domains

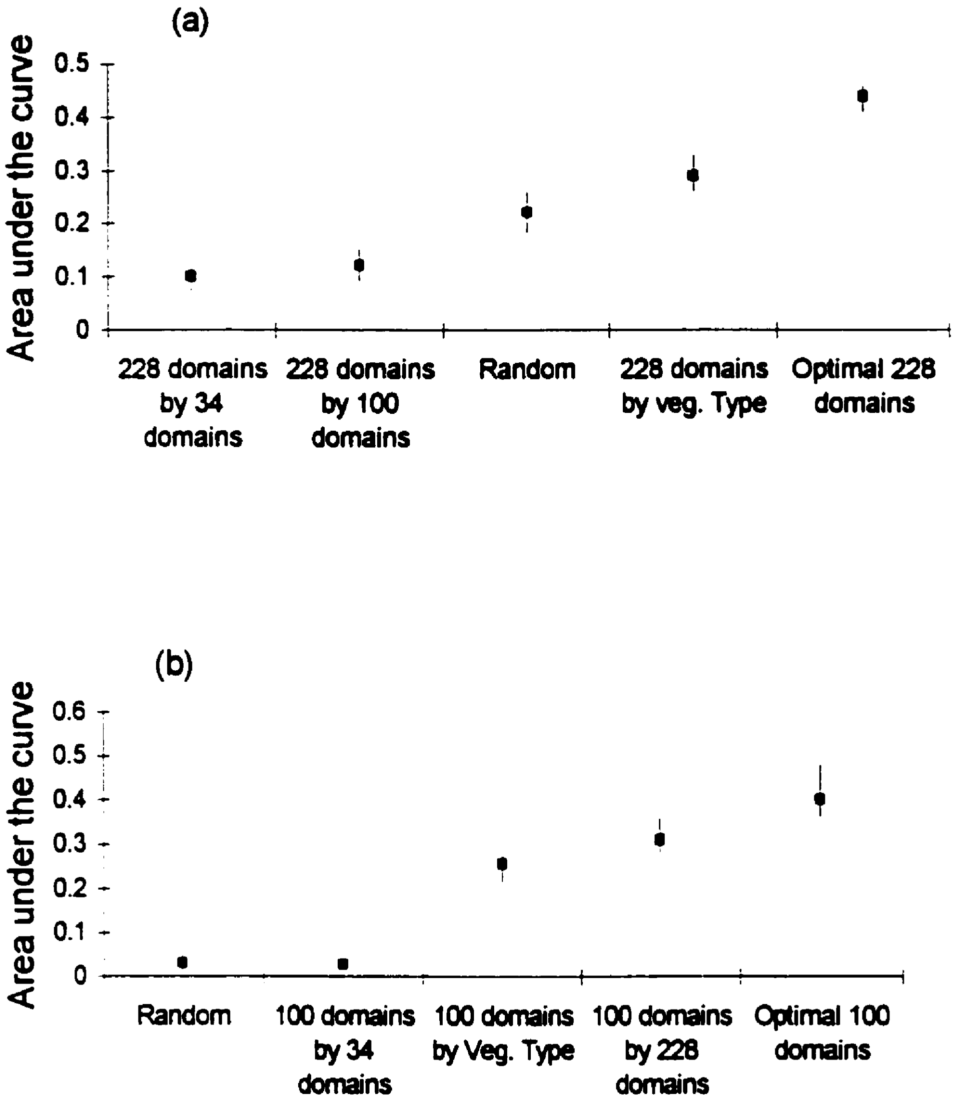
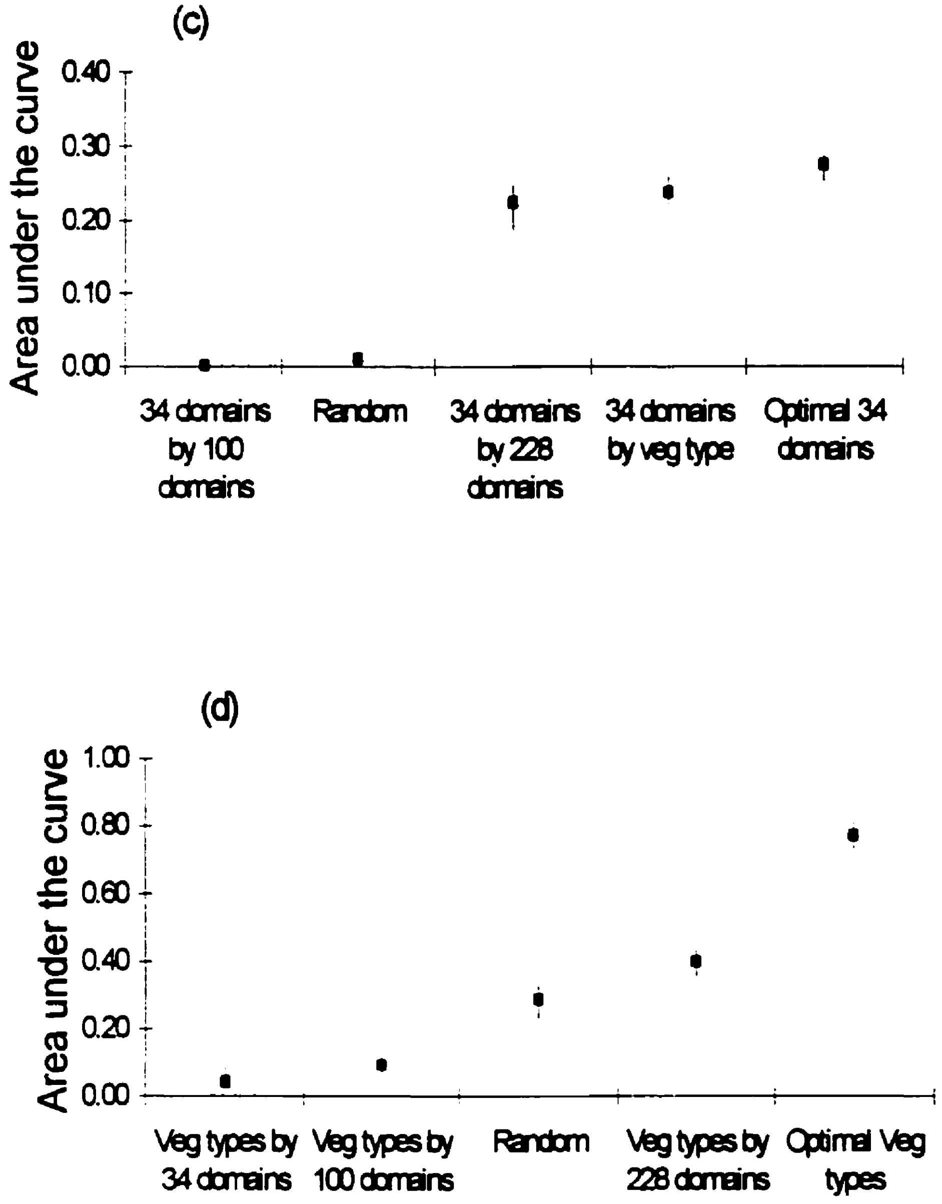


Figure 21: (c) Comparison of Areas 34 Domains; (d) Comparison of Areas Vegetation Classes



When the vegetation map of 34 vegetation classes is visually compared with the environmental domain classification of 34 groups, the domain classification shows similar pattern of divisions with the vegetation map in the Pakaraima Mountains, Kanuku Mountains and Rupununi savanna. However, the environmental domain classification does not distinguish the riverine and riparian habitats along the main rivers of Guyana as a separate domain as in the vegetation map. The domain classification does, however, classify the south-east of the country and north-central forests into many more division than the vegetation map. The lack of correspondence with the environmental domain classifications and the vegetation map in the lowland forest of Guyana may be due to difficulty differentiating low-lying forest types from the LANDSAT images. When the environmental domains are divided further to 100 and 228 classes and compared with the vegetation map, much more division of domains is seen in the central-north forests. The south-east is not as well divided up as the rest of Guyana by the domain classification and this may be due to the lack of accurate rainfall, temperature and lithology data from the area due to the limited access. For example, the mountainous areas in the south-east only become more distinguishable at the 228 domain level. The lack of data for this area is also evident in the vegetation map (Huber *et al.* 1995).

Similarities in the shape and location of environmental domains and vegetation classes end when these surrogate measures of biodiversity are used to prioritise biodiversity sites. The comparison of the maps of the summed irreplaceability values and priority biodiversity sites clearly demonstrates the differences in the priority of grid cells using the different classifications. The greatest differences in the valuation of (measured by summed irreplaceability) and location of priority sites are between the different environmental domain classifications and the vegetation map. The relatively low degree of overlap (13.7-23.4%) between pairs of classifications and between all four (0.78%) indicates that each type of surrogate measure produces a somewhat different result. When irreplaceability values are used there is flexibility in all but the most irreplaceable of sites. Thus, some of the differences may be due to choices made by the algorithm in the location of sites for those grid cells that are less than fully irreplaceable. The only way to test whether the lack of overlap is due to choices in the location of sites or to real differences is by examining how effective a certain surrogate measure is at representing another surrogate measures. In the case of this study, this was done using feature accumulation curves and by comparing the areas under the curves.

The feature accumulation curves and analyses of areas under the accumulation curves provide the only means of evaluating how well each of the classification can "act" as a surrogate for any of the other classifications. In this study, there was a significant difference between the selection of grid cells under optimal conditions, and the selection of grid cells by the other classifications or by random, except in the case of 34 domains. In the case of 34 environmental domains, both vegetation classes and 228 environmental domains were within the range of the optimal, although their mean feature accumulations were lower. This implies that the differences in the classifications are real and these differences lead to different scenarios of priority biodiversity sites. Knowing which, if any, of the classifications is the 'best' to use in conservation decision-making is very difficult, as the number of classifications is somewhat arbitrary and one must operate under the assumption that the abiotic factors chosen for the study reflect biological diversity.

There have been a number of studies in pattern analysis to determine the optimal number of domains for a given set of data, however none of these studies demonstrated a foolproof method; they all made unwarranted assumptions about the data (Belbin 1993a). The estimation of domains is also prone to error from sampling biases (Belbin 1993). To remove some of the arbitrariness of the number of domain classifications, a method was used to "fit" the number of domains to the number of types that could be represented in any 15 % of Guyana. This novel approach, although an improvement on random cut-off numbers, also has an inherent problem. If some of the diversity in the environmental pattern is found below the cut-off of 15 %, then it is lost in the classification. Another problem relating to the classification of domains which cannot be avoided, but may be important, is that equal classes or division of rainfall and temperature may not be equal in determining ecological processes and species distributions. For instance a change from 1000mmm of rain to 1500mm of rain may be insignificant to the vegetation and animal species, however the same change from 2500mm to 3000mm may have a drastic effect on species composition and vegetation distribution. This type of information cannot be incorporated into the domain classification, nor is it well understood in the ecological literature.

In conclusion, the identification of priority biodiversity sites using environmental domain classification and vegetation classes as surrogate measures of biodiversity produced mixed results. On the one hand, the number of grid cells required to represent 15 % of each domain-type or vegetation type varies from 291 grid cells (8.9 %) for 34 domains to 615 (17.3 %) for 228 domains with a mean of 434 grid cells or 12.2 % of the territory of Guyana. And, for the most part, these grid cells are well distributed across the country. Although there is not extensive overlap between the classifications, all classifications select priority biodiversity sites in the Pakaraima Mountains, the Kanuku Mountains and the lowland evergreen forest (rainforest) of the central-north. On the other hand, none of the classifications, with the exception of 34 environmental domains was a good surrogate for the other classifications, some even performed worse than random. Thus, using 3 out of the 4 classifications to identify priority biodiversity sites would severely limit the amount of features of the other classifications captured. This poses a problem if it can be argued that all four classifications are equally good as surrogate measures of biodiversity. As mentioned above, the classification of environmental domains and vegetation classes is somewhat arbitrary and untested. One way of examining the effectiveness of these types of biodiversity surrogates is to see how many known species they capture when they are used to select priority biodiversity sites. This evaluation is carried out in the next chapter when species distributions are examined.

Chapter Five

Species as a Measure of Biodiversity

5.1 INTRODUCTION

The most frequently used measure of biodiversity is species richness, defined here as the total number of species recorded in a grid cell. This measure of biodiversity is commonly used in conservation planning as a tool to determine where priority biodiversity sites should be located (Reid 1998). Sites with greater species richness have generally been considered more important for conservation than the sites deemed "species-poor" (Myers 1988, 1990, Miettermeir 1988, NcNeeley *et al.* 1990, WCMC 1992). The major limitation to this approach is the lack of information on individual species distribution in a given area. Given that complete inventories of species are impractical, particularly in species-rich tropical areas, the utility of species richness and other species-based approaches depends on the extent to which results from limited data sets can be generalised. If data can be generalised, two questions can be asked. Can inferences about poorly known areas be made on the basis of well-studied areas? And, can inferences about poorly known species or taxa be derived from indicator species' distributions?

The use of indicator species groups as surrogates for other taxonomic groups relies on the premise that across a given area, the species richness of a well-studied species group is highly correlated with the species richness of a lesser-studied group (Terbough and Winters 1983, Scott *et al.* 1987, Schall and Pianka 1987, Mittermeier and Werner 1990, McNeely *et al.* 1990, Myers 1990, Gentry 1992, Pearson and Cassola 1992, WCMC 1992, Thirgood and Heath 1994, Gaston 1994, Gaston and Williams 1996, Prendergast *et al.* 1999). The "surrogacy value" of different taxonomic groups can be measured by comparing the efficiency of each group as a surrogate for the other groups. For instance, if ferns were used to select the priority biodiversity sites for birds, they would be considered very efficient if they captured all the bird species in the same number of grid cells as when birds were used to select priority sites for birds. By looking at the efficiency of different surogate-groups at representing a target taxonomic group, conclusions can be made on the performance of those groups to represent biodiversity. A critical question in conservation decision-making concerns the congruence of species-based surrogates. Several studies have concluded that there is little overlap in priority biodiversity sites among taxonomic groups (Prendergast *et al.* 1993, Dobson *et al.* 1997, Van Jaarsveld *et al.* 1998), however, other studies do show overlap amongst taxonomic groups (Kerr 1997, Howard *et al.* 1998).

This chapter examines the patterns of species distribution in Guyana and investigates different species-based surrogate measures of biodiversity. Species richness and the restricted range values of species (a measure of endemism) in Guyana are calculated and comparisons of different taxonomic groups are made. Recorded and modelled species locational data are then used to select sets of priority biodiversity sites based on species richness and irreplaceability. The surrogacy values of the different richness and irreplaceability sets are compared for several taxonomic groups and the surrogacy values of richness and irreplaceability sets are then compared with those derived for environmental domains and vegetation classes.

Although there have been several studies on the usefulness of species-based surrogates, the surrogacy values of irreplaceability sets have never been assessed. This study differs from previous studies by using irreplaceability to measure biodiversity importance and by looking at the efficiency of the different species-based surrogate measures, not just the overlap in sites among surrogate measures. As irreplaceability is being used as a "real-world" tool for conservation planning, it is important to test how many species are captured in the sites identified using this surrogate. In addition, this study differs from previous studies by comparing the priority biodiversity sites selected for different taxonomic groups with those selected using classifications of environmental domains and vegetation classes. Finally, data and results on surrogacy and irreplaceability presented in this chapter are the first for any tropical area in South America and hence, are important for comparison with African, European and North American results.

5.1.1 Species Survey Data

A problem with using species data as a measure of biodiversity, especially to determine the location of priority biodiversity sites, is the impact of data quality. As discussed in chapter two, at least three types of gaps exist with regards to data describing the distribution of species: a) geographical gaps, as field surveys can only afford to sample a small part of a given region; b) temporal gaps, because sites are usually surveyed once or a small number of times and may not describe variation over time; and c) taxonomic gaps, as not all taxonomic groups are sampled or even known (Ferrier 1997). These gaps pose a problem for selecting priority biodiversity sites, hence the use of "surrogate" measures of biodiversity. Since species data are most commonly used to select priority areas, it is imperative that the best species data available be used. A recent study by Freitag and Van Jaarsveld (1998) using data from South Africa, looked at the impact of survey intensity, extent, and taxonomic diversity on the selection of priority biodiversity sites. In an attempt to duplicate the effects of incomplete surveys, they systematically deleted species from existing records and used the remaining data to select priority sites. They found that the systematic deletion of species records greatly varied the location and number of selected sites. In most cases, field data are limited by financial and time constraints and although researchers all agree that the more species data the better, supplementing existing databases is rarely an option.

To reduce the effects of small sample sizes and sampling biases, modelling based on data interpolation is typically used to estimate the expected distribution of each species. Data interpolation techniques have been widely used in the last ten years to augment species survey data (Nix 1982, Nix 1986, Austin and Margules 1996, Margules *et al.* 1988, Scott *et al.* 1988, Walker 1990, Lindenmayer *et al.* 1991, Nix and Switzer 1991, Carpenter *et al.* 1993, Scott *et al.* 1993, Butterfield *et al.* 1994, Margules and Austin 1994). There are several modelling techniques that are commonly used depending upon the type of survey data available. First, one of the simplest but well tested is based on the Gap Analysis technique pioneered in Idaho that matches species presence/absence with vegetation type and models vertebrate distributions based on vegetation type (Scott *et al.* 1993, Butterfield *et al.* 1994). Second, when other types of environmental features are available such as climate, geology and vegetation, there are several techniques that are used to model distributional data. With species presence-only datasets, the techniques include: a) decision-tree modelling based on partitioning of data based on a tree-structured set of rules, (Walker and Cocks 1991, Stockwell and Peters 1999); b) profile matching, a system for predicting species distribution based on the profile of known species records in relation to climatic variables (Nix 1986, Busby 1986, 1991, Lindenmayer *et al.* 1991, Nix and Switzer 1991, Carpenter *et al.* 1993); and c) genetic algorithms, based on a set of rules derived using optimisation techniques (Stockwell and Peters 1999). Finally, when surveys contain presence/absence data, generalised linear models and generalised additive models have been used (Austin *et al.* 1984, Nicholls 1989, Nicholls 1991, Lindenmayer *et al.* 1991, Yee and Mitchell 1991, Ferrier and Watson 1997). All of these methods can help researchers infer expected distribution patterns for sites for which there may be no survey data. This additional information can be used in the selection of priority biodiversity sites. However, poor results can be obtained when insufficient data are used.

5.1.2 Species-based Measures of Biodiversity

5.1.2.1 Species Richness

As discussed previously, species richness and other species-based measures of biodiversity such as restrictedness are the most common data used for conservation decision-making. One reason species-based measures are popular, is that they appear to be simple and a direct measure of biodiversity (Williams *et al.* 1996). Examples of conservation strategies that have sought areas to maximise the number of species include: a) the Gap Analysis in the United States (Scott *et al.* 1987, Burley 1988, Scott *et al.* 1993), which is based on patterns of vertebrate distributions and their relationship to specific habitats; b) the megadiversity countries analysis, which is based on the small number of countries deemed to contain the majority of the world's biodiversity (Mittermeier and Werner 1990, McNeely *et al.* 1990); c) WCMC's (1992) regional assessment of higher taxa, which is based on assessing the 25 most biodiverse countries; and d) USAID's (1995) regionalisation of Latin America and the Caribbean, which is based on the species richness of several taxonomic groups into "Regional Habitat Units". Some approaches, such as the Gap Analysis, (Scott *et al.* 1993, Butterfield *et al.* 1994) use a combination of actual species distributions and other layers of information such as vegetation type, whereas other approaches use only the actual number of species found at a given location (Mittermeir and Werner 1990, NcNeeley *et al.* 1990, USAID 1995). However, species richness is not as simple as it appears, as the measure itself depends on: a) recognition and identification of the species in a given area; b) good knowledge of species distributions; and c) adequate spatial and temporal sampling (Williams *et al.* 1996).

5.1.2.2 Species Restrictedness

As with species richness, the term endemism is applied in an inconsistent manner. Species that are found in a particular region and nowhere else are said to be endemic to that region, however endemism is a relative concept to the spatial scale of analysis (Cowling and Samways 1995). Guyana is only one of four countries that lies across the Guiana Shield and it is difficult to distinguish species that are endemic only to Guyana and not the entire Shield. A more practical approach to defining endemism, especially for a country like Guyana, has been to calculate the restricted range value of a species based on the total number of grid cells/quadrats or areas the species is found in over a given area (William *et al.*

1996 Kerr 1997). It has been argued that regions of high endemism or restricted range values should receive priority in conservation decision-making, as protecting species that are unique to a region may be more important than protecting areas which are just rich in a variety of commonly found species (Myers 1988, 1990, Bibby *et al.* 1992).

5.1.2.3 Hotspots

A large portion of the world's species can be conserved by protecting a relatively small area known as a biodiversity "hotspots" (Myers 1988 1990, Gentry 1992, Pearson and Cassola 1992, Prendergast *et al.* 1993). Hotspots of biodiversity are defined either as areas of exceptional endemism and richness which are threatened by human-induced activities (Myers 1988) or the top 5% of cells within a given area which are the most species-rich or contain the most endemic species (Prendergast *et al.* 1993, Williams *et al.* 1994). Myers (1988) and WCMC (1992) identified 18 hotspots world-wide which contained exceptional levels of endemism and species richness and faced a high rate of habitat modification. These areas contain over 20 % of the world's plant species in less then 0.5 % of the total land surface. Prendergast *et al.* (1993), Lawton *et al.* (1994) and Williams *et al.* (1994) applied the term "hotspots" to grid cells in Great Britain that contained the most species or the most endemic (range-size rarity) species for various taxonomic groups. Prendergast *et al.*'s (1993) study of species groups in Great Britain found that the overlap of species-rich hotspots was low between taxonomic groups, however if one taxon was used to select sites for a protected areas network, at least 50 % of the species in that taxon and approximately 50 % of the species in the other taxonomic groups studied would be protected. Similarly, restricted range species were more likely to be found in species-rich hotspots than in randomly selected grid cells (Prendergast *et al.* 1993). However, they found that most hotspots did not capture rare species. They conclude that this may be in part due to the fragmentation of the British landscape that had left many rare species in isolated pockets.

5.1.2.4 Cross-Taxon Congruency

In recent years, several studies have also looked at the cross-taxon congruence of sites, with the goal of identifying indicator taxonomic groups that could be used to predict the distribution of other taxonomic groups. These studies have produced mixed results. Prendergast *et al.* (1993) and Lawton *et al.* (1994) showed cross-taxon congruence for five groups of species (birds, liverworts, aquatic plants, dragonflies and butterflies) in Great Britain was low (range 0-34 %). Congruence was especially low between groups with different ecological requirements. They concluded that at the spatial resolution of 100 km^2 grids, areas of high species richness coincided much less than excepted (Prendergast et al 1993, Lawton *et al.* 1994). Prendergast *et al.* (1993) suggested that British data may not be representative of other areas of the world, as Britain is an island that has a very fragmented and modified landscape. Studies from other locations at larger spatial scales (continental) have shown significant correlations among several taxonomic groups. Pearson and Cassola (1992) showed that the relationship between tiger beetles and breeding birds was positively correlated in North America, the Indian subcontinent and Australia. Tiger beetles and butterflies were also positively correlated for North America and Australia (Pearson and Cassola 1992). Currie (1991) showed amphibian richness was clearly related to tree richness across North America, whereas other vertebrate classes showed no relationship with tree richness. Kerr (1997) observed only weak correlations in species richness between taxonomic groups for mammals, Lasioglossum, Papilionidae and Plusiinae across North America. Studies from two areas in Africa (Uganda and South Africa) (Howard *et al.* 1998 and Van Jaarsveld *et al.* 1998) have presented the best data to date for tropical regions. They have convincingly shown that for these areas there is little congruency between different taxonomic groups for species richness, rare species, hotspots and coldspots (areas with the lowest number of species)(Howard *et al.* 1998 and Van Jaarsveld *et al.* 1998). Although for countries in the Indo-Pacific region, Dinerstein and Wikramanayake (1993) showed that mammal species richness and bird species richness were strongly correlated with vascular plant species richness. The difference in results may be due to the scale at which the analyses were done.

Dinerstein and Wikramanayake (1993) looked at the whole Indo-Pacific region, whereas the Howard *et al.* (1998) and Van Jaarsveld *et al.* (1998) only examined a portion of a country.

5.1.2.5 Congruency between Restrictedness and Species Richness

For the congruency between restrictedness and species richness, Prendergast *et al.* (1993) showed that in Great Britain, areas with the restrictedness did not overlap with those areas with the highest species richness for the taxonomic groups examined. Conversely, Kerr (1997) examined the relationship between restrictedness and species richness for all mammals across North America and found a strong positive correlation between species richness and restrictedness however, he found only weak correlations in other between-taxa comparison of species richness and restrictedness. In contrast, he found no cross-taxon congruence for restrictedness. A study on the global patterns of mammalian diversity showed that the number of endemic species was only weakly correlated with both increasing land area and species richness (Ceballos and Brown 1995). For tropical areas, Dinerstein and Wakramanayake (1993) showed restrictedness and species richness for mammals, birds and reptiles were only weakly correlated in the Indo-Pacific region. An analysis of the location of Endemic Bird Areas (EBAs) and other important areas for vertebrate restrictedness at the continental scale, showed some congruency in Africa between EBAs and species richness of other taxonomic groups. High congruency between restrictedness and species richness was demonstrated for groups studied on the Caribbean islands (only a few are large enough to have many endemics), and a congruency of over 50 % was demonstrated for Central, South and North America and Asia, however no quantitative analyses were done and analyses were hindered in many places by lack of reliable data (Thirgood and Heath 1994). Evidence now exists to suggest cross-taxon congruence of species richness and restrictedness on a large geographical scale, but it appears that this congruence is lost on finer geographical scales, which clearly poses a problem for designing protected areas. These findings put into question the value of using species richness or restrictedness for selecting priority biodiversity sites. One important issue that is raised by all of the studies mentioned above, is that even if the data showed good cross-taxon congruency and congruency between species richness and restrictedness, there is little agreement in the literature on which species-based surrogate measure of biodiversity should be used.

5.1.3 Selection of Priority Biodiversity Sites Using Species-Based Data

5.1.3.1 Complementarity

The primary goal of a network of priority biodiversity sites is to represent the range of biodiversity found within a region. As discussed previously, priority biodiversity sites have traditionally been selected using information on species richness and restrictedness. One of the main drawbacks with using species richness or restrictedness to select priority biodiversity sites for conservation is that they do not provide any means of ensuring that *different* species in an area are conserved. A site might be relatively species-poor, but if it adds the most species not already represented, then it may be the most important in terms of conservation (Flather *et al.* 1997). Thus, selecting priority biodiversity sites based on the degree of overlap of species among sites has gained a lot of recognition in the past few years (e.g. Kirkpatrick 1983, Ackery and Vane-Wright 1984, Margules and Nicholls 1988, Vane-Wright *et al.* 1991, Pressey *et al.* 1993, Margules *et al.* 1994, Kershaw *et al.* 1994, Underhill 1994, Howard *et al.* 1998, Van Jaarsveld *et al.* 1998). The term "complementarity" is used to describe the degree to which a grid cell or site contributes otherwise unrepresented species to a set of grid cells or sites (Vane-Wright *et al.* 1991, Pressey *et al.* 1993, Margules *et al.* 1994). It is possible to represent many more species using species richness or restricted range values *and* complementarity to select the same number of sites, as sites selected only using hotspots (Howard *et al.* 1998, Van Jaarsveld *et al.* 1998, Lombard *et al.* 1999). Alternatively, one study suggested that complementarity alone be applied and compared for indicator species groups rather than measures of richness and restrictedness (Williams *et al.* 1996). To look at the results when complementarity alone was used, Williams *et al.* (1996) applied a simple heuristic algorithm to seek to represent all species of British birds at least once in the least number of grid cells. Although Williams *et al.* (1996a) did not compare cross-taxon congruence of complementarity, they did propose that complementarity scores be used as a tool for selecting priority biodiversity sites. This concept has been applied in the two recent African studies. In the case of Uganda, the cross-taxon complementarity congruence was consistently high and this was attributed to the similar patterns of biogeography across the selected taxa (Howard *et al.* 1998). However, results from a similar study in South Africa showed little support for the notion that species complementarity was congruent across taxa (Van Jaarsveld *et al.* 1998). The difference may be due to the way complementarity was measured and the differences in the biogeography. The study sites in the Ugandan study shared a similar biogeography (Howard *et al.* 1998), whereas the South African sites differed quite a bit in the habitats they covered (Van Jaarsveld *et al.* 1998).

5.1.3.2 Irreplaceability

Comparisons of sites selected using the combination of species richness and complementarity have shown that using the principle of complementarity for selecting sites greatly increases the number of species conserved and captures a great deal more rare species (Williams et. al 1996, Howard *et al.* 1998, Van Jaarsveld *et al.* 1998). Taking the idea of complementarity one step further, Pressey *et al.* (1993, 1994) devised an index of irreplaceability, which measures the relative irreplaceability value, or potential contribution of a site to a conservation target. One of the advantages to using an index of irreplaceability to identify priority biodiversity sites is that sites can be selected using environmental domains and vegetation classes, as shown in the previous chapter, or using species locality data. One of the disadvantages is that there must be sufficient data and data must cover the entire geographical area under study (Pressey 1999).

This chapter expands on previous studies and examines congruence patterns for different taxonomic groups using species richness, restricted-range value and irreplaceability as criteria for selecting priority biodiversity sites. Congruence is measured both by the degree of overlap as in previous studies, but also by the percent of other taxonomic groups (surrogate-groups) captured when priority sites are selected using one taxonomic group (target-group). The accumulation of species for the target-group and surrogate-groups is measured by deriving an index for the area under the species accumulation curve (Ferrier and Watson 1997). Priority biodiversity sites selected using different kinds of data are then compared and differences and similarities discussed.

5.2 METHODS

5.2.1 Data Collection

To determine the distribution of the plant and animal species in Guyana would be a near impossible task. At present, data do not exist for the majority of invertebrates. There are 7,000 species of flowering plants alone (Boggan *et al.* 1997). The best data are those collected and maintained by the Smithsonian Institution's Biological Diversity of the Guianas Program. This database contains georeferenced information and was assembled and curated by Dr. Vicki Funk, Director of the Biological Diversity of the Guianas Program. Dr. Funk supervised each field collector over the past 17 years and has applied consistent data standards. Data were collected from both historical collections of Guyana housed at museums and herbaria around the world and from the field collections of the Smithsonian Institution. The majority of the data came from the Smithsonian Institution, USA; the Royal Botanic Garden at Kew, England; the British Museum of Natural History, England; the University of Utrect Herbarium, the Netherlands; the Royal Ontario Museum, Canada; the University of Guyana, Guyana, and the American Museum of Natural History, USA. One feature of this database is that it is all specimen-base and no observational data are included. This is important for the verification of taxa. A sample of the structure and information in the database is found in Appendix 1.

Data on species distributions were entered into a DBase IV database especially designed for the Guyana database (Funk *et al.* 1999). If a geocode was not already assigned to each species record, the latitude and longitude were determined if possible (Funk *et al.* 1999). Only species records which were geocoded in the database were included (31% of initial records were discarded). In total, 5,123 species (25,111 records) were used, including 4,482 species of plants and 641 species of animals. For all of the analyses except the comparison of species richness, only a reduced dataset of 320 species were used, as only this number of species had 10 or greater locational points across Guyana and this was a requirement for further modelling.

To examine cross-taxon congruence of species richness, restricted range values and irreplaceability, ten taxonomic groups were chosen. These taxonomic groups were selected based on three criteria (Funk *et al.* 1999). First, that a specialist of that group be available for consultation. Second, that the groups could be found in as many vegetation classes in the country as possible. Third, to evaluate restricted range species and species with wide distributions, that at least one genus in each group was restricted in its distribution and at least one genus was widespread in its distribution. The ten groups chosen span a wide variety of organisms, and consist of 2-11 (mean=3) genera on average. The groups are: mammals, birds, amphibians, orchids, sedges, melastomes, legumes, understorey trees (family Chrysobalanaceae), large emergent trees (family Lecythidaceae – the Brazil nut family), and ferns. In total, 132 species of the 320 species reduced dataset fall within these groups. Table 7 lists the number of species for each taxonomic group.

Table 7 - Number of species and genera used for each taxonomic group

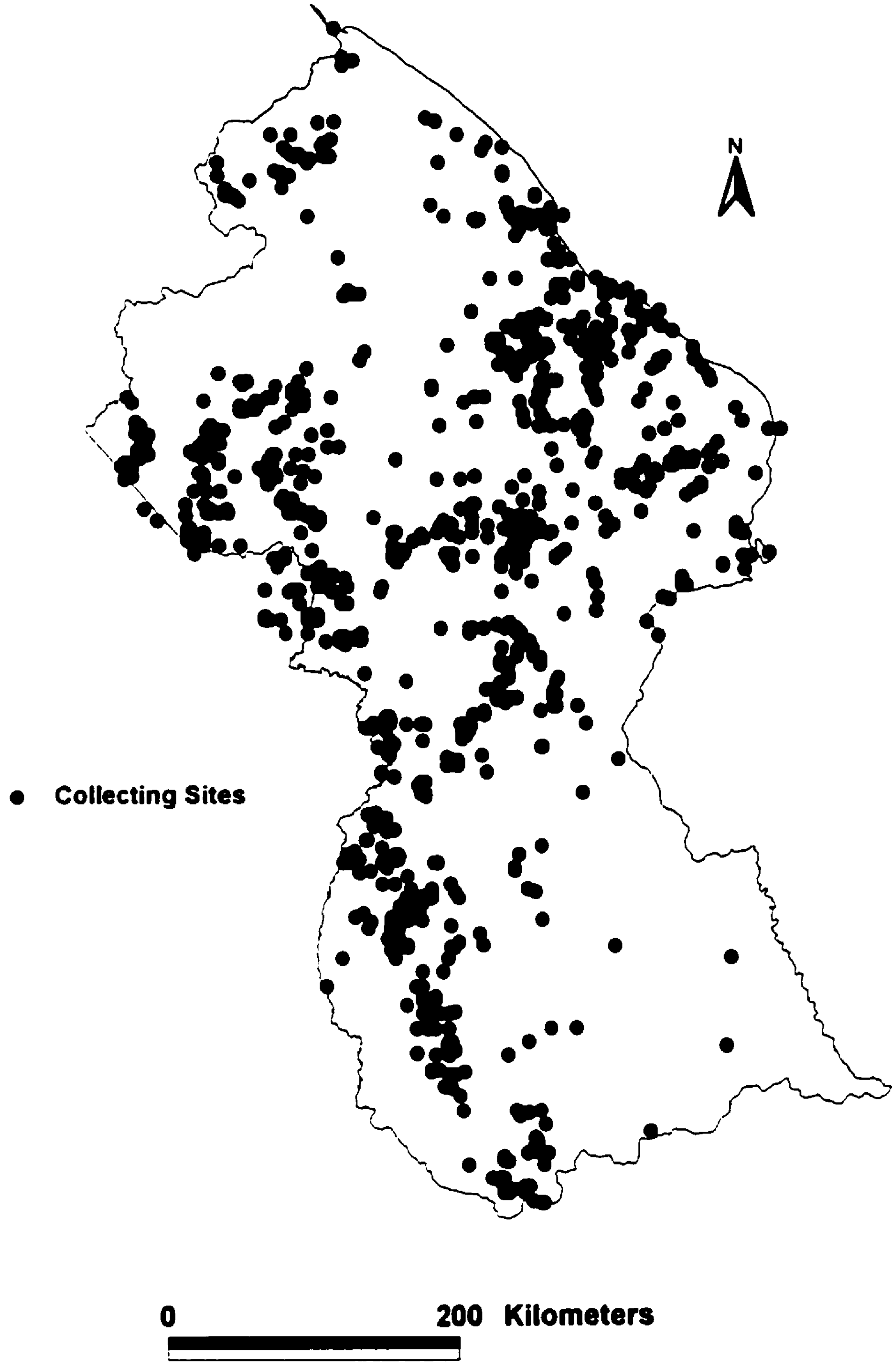
Taxonomic Group	**Number of Species**	**Number of Genera**
Birds	33	11
Understorey trees	12	3
Ferns	13	4
Amphibians	6	4
Emergent trees	6	2
Legumes	12	2
Mammals	7	6
Melastomes	6	3
Orchids	18	9
Sedges	19	2
Total	132	46

Although the south-east part of Guyana is believed to be very species-rich, access to the area is restricted due to a border dispute with Suriname and, with the exception of two mammal collecting expeditions, no one has brought out specimens from this region. Because of the lack of data, it was decided to use the results for this part of Guyana with extreme caution.

5.2.2. Modelling

As expected in a country with very few roads, collection localities were clustered mostly around airstrips and along rivers. To enhance the geographical spread of the dataset, a new dataset was created with data that were modelled to obtain both recorded and predicted distributions of species. Species locational records were mapped onto a 16 km^2 grid of Guyana (Figure 22). To determine the minimum number of species records required to model species distribution, maps were produced of modelled distributions using different number of locational records.

Figure 22: Collecting Localities in Guyana

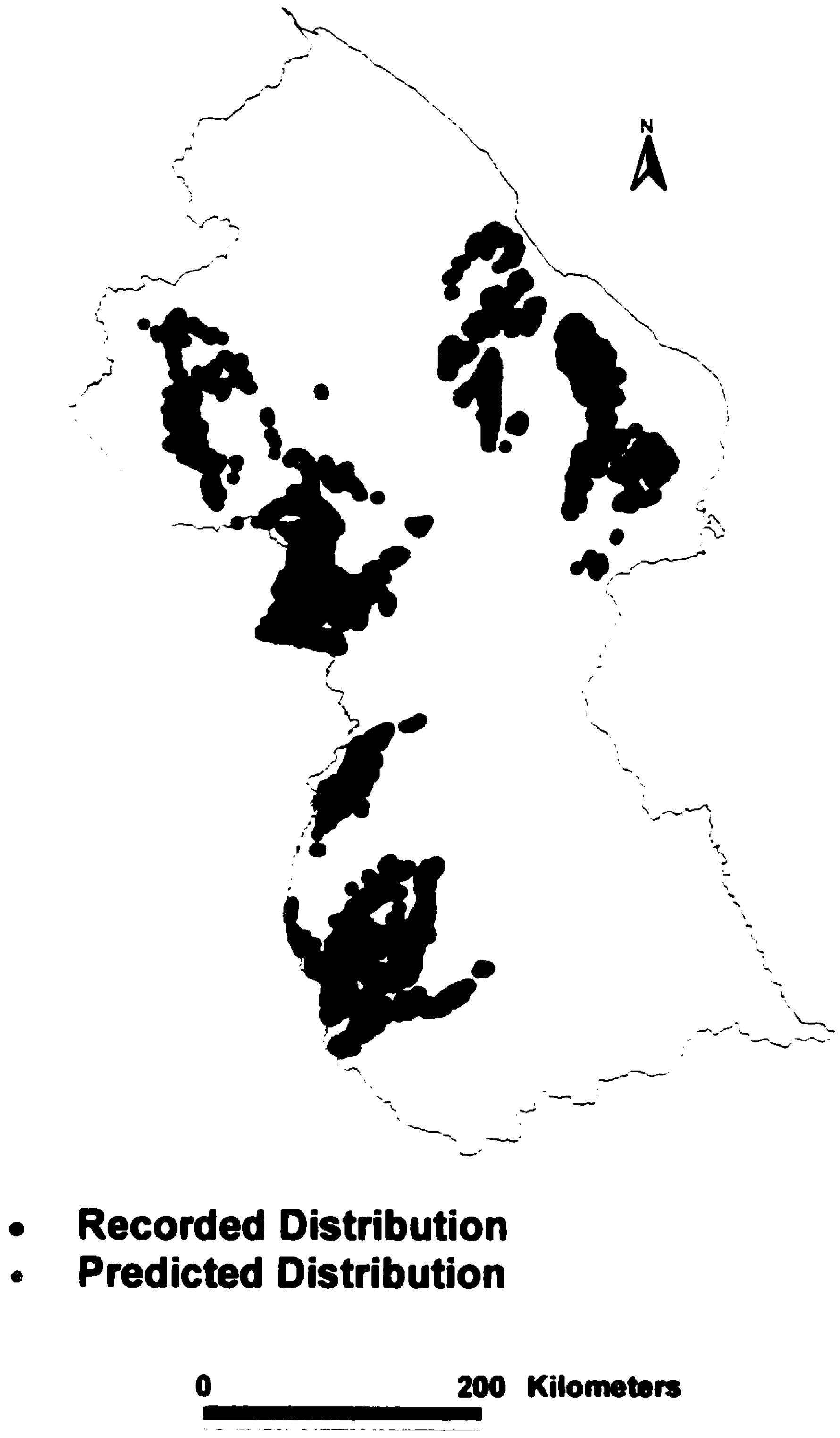


locational points were decided upon. An expert on the flora and fauna of Guyana, Dr. Vicki Funk, was asked to examine them. A minimum number of ten (10) locational records were included in the analysis. Species distributions were modelled using DOMAIN (version 1.4, 1997), a spatial modelling tool that predicts species distribution based on a point-to-point similarity metric, which assigns a classification value to a candidate site based on the proximity in environmental space of the most similar site (Carpenter *et al.* 1993). The steps taken to model the potential distribution of species were: (a) the variables for modelling species distributions were chosen using Principal Component Analysis (Statistica 1999) to evaluate the least autocorrelated variables. The variables chosen were the DEM, vegetation map, lithology map and the mean monthly rainfall of the driest month (October). These variables were verified by an expert, Dr. Vicki Funk, as relevant to the distribution of plants and animals in Guyana. The methodology used to obtain the DEM, climate layers, lithology and vegetation classification is described in chapter 4. (b) Each species was modelled using the DOMAIN program using the selected variables. (c) A similarity map was produced for each species that showed the likelihood of the species being present in a given area. (d) The similarity maps of the modelled potential distribution of each species were reclassified in Idrisi (version 2.0 Clark University 1997), to show the actual distribution and the modelled distributions with a similarity value of 95 % or greater (Figure 23 for an example). A similarity value of 95 % or greater was chosen as a conservative cut-off point for the potential distribution of a species.

5.2.3. Species Richness

Species richness was defined as the number of species occurring in each 4 km x 4 km grid cell. The total number of 16 km^2 grid cells was 13,751. Species richness maps were produced using ArcView 3.1 (ESRI 1998) for all species (5,123 species) by overlaying the distribution of each individual species and using the Boolean addition of each map. The richness map for 5,123 species was compared

Figure 23: Example of Recorded and Predicted Distribution of a Species



with that for the reduced dataset of 320 species by visually examining the distribution of species. In the case of the reduced dataset of 320 species, species richness was calculated using both the recorded species distribution and predicted distribution (95% or greater similarity values) grid maps of individual species. Distribution maps were produced in Idrisi (version 2.0 Clark University 1997), and the maps of each species were overlaid using Boolean operators to produce species richness maps. To test the accuracy of the predicted data, a cross-validation procedure was used where the actual distributional dataset for each taxonomic group was randomly divided into two subsets (of equal size) (Ferrier and Watson 1997, Stockwell and Peters 1999). The modelling procedure was performed on one of the subsets and was then tested against the other subset. This procedure has been used in other studies to test the performance of predictive species models (Stockwell and Peters 1999). The predicted distribution maps shows a more complete coverage of the country, but the cross-validation showed that the modelling technique picked up greater than 92 % of the actual locations. On this basis, both the actual and predicted distribution maps were used for further analyses.

5.2.4 Restricted Range

As discussed previously, endemism is difficult to measure within the political boundaries of Guyana. Rather than use endemism as a measure, an index on how restricted the range of a species is in the dataset (and hence in Guyana) was used. The main drawback to this approach is that it can fail to distinguish species that may be highly restricted geographically instead of restricted numerically. However, in the case of Guyana this is hardly a drawback because little is known about geographically restricted species.

The restricted range index was calculated for each species and for each grid in the reduced dataset. The restricted range index was calculated by counting the number of grid cells in which each species occurred, taking its inverse and summing the total for each grid cell, as follows:

$$\text{Restricted Range Index} = \sum_{i=1}^{S} Q^{-1}$$

where S is the total number of species in the taxonomic group under consideration (e.g. mammal, sedge), and Q is the total number of grid cells included in each species range. Thus, species with very restricted ranges had higher scores, with the most restricted species (ones which occurred in only one grid cell) scoring 1.0 on the restricted range scale. Data were transformed log $(x+1)$ to normalise the variance. Spearman rank correlations were used to investigate the richness-restricted range distribution relationship for each taxonomic group, all plant groups together, all animal groups together, and all species summed together

5.2.5 Hotspots

"Hotspots" of species richness and restricted range species were calculated for the ten taxonomic groups and for all species combined in the reduced datasets. Species richness hotspots were calculated following Prendergast *et al.* (1993) and Lawton *et al.* (1994) as the top 5 % of grid cells with the highest species richness; and restricted range hotspots were calculated as the top 5% of grid cells with the highest restricted range value (e.g. containing the most restricted species). The spatial overlap between hotspots was calculated using the Jaccard coefficient calculated as the [number of grids shared between taxon A and B/(number of additional grids cells for taxon A + number of additional grid cells for taxon B) x 100] (Van Jaarsveld *et al.* 1998).

5.2.6 Irreplaceability

Irreplaceability, as described in Chapters 2 and 3, was measured using C-Plan (NSW NPWS 1999). Because of computational demands, only the reduced dataset of 320 and the data for the 10 taxonomic groups were used to map irreplaceability values. The summed irreplaceability, the sum of irreplaceability values for each grid cell for each species was used to rank grid cells. In this case, a target of three occurrences of each species was used. The choice of three occurrences as a target builds some redundancy into the representation of species. The map of summed irreplaceability provides an initial "snapshot" of the irreplaceability across Guyana. It indicates the rank order of sites based on their initial summed irreplaceability. A map of priority biodiversity sites derived using minimum set algorithms differs from the map of summed irreplaceability because when minimum set algorithms are used to select priority biodiversity sites, the grid cell with the highest summed irreplaceability is selected first. The summed irreplaceability of the remaining grid cell is then re-calculated and the grid cell with the next highest summed irreplaceability is chosen until the target is met. Since the summed irreplaceability is re-calculated each time a grid cell is removed, the importance of the grid cells may change with regards to the species already captured in the selection of other cells.

5.2.7 Priority Biodiversity Site Selection

Priority biodiversity sites were selected using two criteria: a) species richness; and b) summed irreplaceability. Site-selection algorithms were used to select priority biodiversity sites. The site-selection algorithm was built from within C-Plan and the resulting maps were output into ArcView (ESRI 1998). For species richness, priority biodiversity sites were selected in the order of the most species-rich hotspot (or top 5 % of the most-species rich grid cells) until all hotspots were included in the selected sites. For summed irreplaceability values, the grid cell with the highest summed irreplaceability was selected first followed by the cell with the next highest summed irreplaceability recalculated each time a cell was selected. In the case of ties, the first grid cell in the tie was chosen. The algorithm stopped once all species were represented 3 times. Sites selected using the different criteria were compared visually and the percent of overlap in sites was measured using the Jaccard coefficient.

5.2.8 Cross-Taxon Surrogacy

The efficiency of taxonomic groups to act as surrogates for each other was investigated using site-selection algorithms based on summed irreplaceability. A separate algorithm was run for each taxonomic group and maps were generated for each run. The rules of the algorithm were altered so that a "target" taxonomic group was chosen each time and sites were selected based on the highest summed irreplaceability values of the selected target-group. The algorithm was run until all species were represented at least 3 times. The accumulation of species in the other taxonomic groups was recorded and plotted along with the accumulation of species for the target-group. An examination of how well the other taxonomic groups acted as surrogates for a particular group was carried out by comparing the optimum accumulation curve (the accumulation curve of the target taxon in question when it is used to selected sites) with the curves generated when other taxonomic groups are used to select sites and the accumulation of a particular taxonomic group is recorded (*i.e.* the accumulation of birds when ferns are used to select sites) and a random curve. Sets of sites selected at random were generated using an algorithm designed to produce a random set within C-Plan. The random curve was generated from 1000 random runs of the algorithm.

A species accumulation index was calculated as the area under the curve for the graph of species accumulation each taxonomic group (after Ferrier and Watson 1997). The species accumulation index was compared for the target-taxon and the other taxonomic groups as surrogate-taxon, as well as the random run. Confidence limits (97.5 % - 2.5 %) were derived using a bootstrapping technique which ran 1000 replacement runs for each combination (Ferrier and Watson 1997).

5.2.9 Comparison with Environmental Domains and Vegetation classes

The overlap of the minimum set of grid cells selected using environmental domains, vegetation classes and the summed irreplaceability of species were compared using the Jaccard coefficient (see Chapter 3 for description of environmental domains and vegetation classes). Although actual overlap itself is not necessarily a good indicator of how well the environmental domains and vegetation classes capture the various species, it does indicate how much overlap there is between selected sites. To test whether the environmental domain classification and the vegetation classes captured any of the species records, a minimum set algorithm was run using summed irreplaceability for the different environmental domains and vegetation classes. The accumulation of species using the reduced dataset of 320 species was examined. In this case, the algorithm stopped when 3 occurrences of each domain or vegetation type were selected and not when all the features (domains, vegetation classes and species) were represented. For instance, if all the species could be represented three times before all the sites were selected to represent the environmental domain or vegetation classes, then the domain or vegetation classes would be effective in capturing all the species. Conversely, if all the sites were selected for the environmental domain or vegetation class and each species was not represented three times, than the domains or vegetation classes would not be effective in capturing the species. Finally, the percent of vegetation classes captured when all plant species in the reduced dataset were used to select priority biodiversity sites was measured.

5.3 RESULTS

5.3.1.Species Richness Distribution

5.3.1.1.Full Dataset

The species richness based on the full dataset across the 13,751 grid cells (16 km^2) ranged from 1 to 1505 species (Figure 24). The sites with the highest species richness were scattered throughout the country, with the highest at Kaieteur Falls, followed by Bartica, Mt. Roraima, Mt. Ayanganna, the Pakaraima Mountains, the Cuyuni river, Matthews Ridge, the Kanuku Mountains, and sites around Georgetown and Dadanawa. There did not appear to be an obvious species richness gradient from east to west or north to south.

5.3.1.2.Reduced Dataset

The distribution of actual and predicted species richness for the reduced dataset for the 16 km^2 grid cells ranged from 1 to 148 (Fig. 25). Only 0.15 % of the total grid cells had high species richness (127-148 species). Conversely, 42 % had low species richness (1-21 species). The sites with the highest species richness for the large dataset overlapped greater than 80 % of the time with the reduced dataset. In this case too, the sites with the highest species richness were scattered throughout the country, with the highest at Kaieteur Falls, followed by Kurupukari, Bartica, Surama, Mt. Roraima, Mt. Ayanganna, the Pakaraima Mounatins, the Cuyuni river area, Shell Beach area, Matthews Ridge, the Kanuku Mountains, and sites around Georgetown and Dadanawa.

Figure 24: Species Richness using Dataset of 5,123 Species

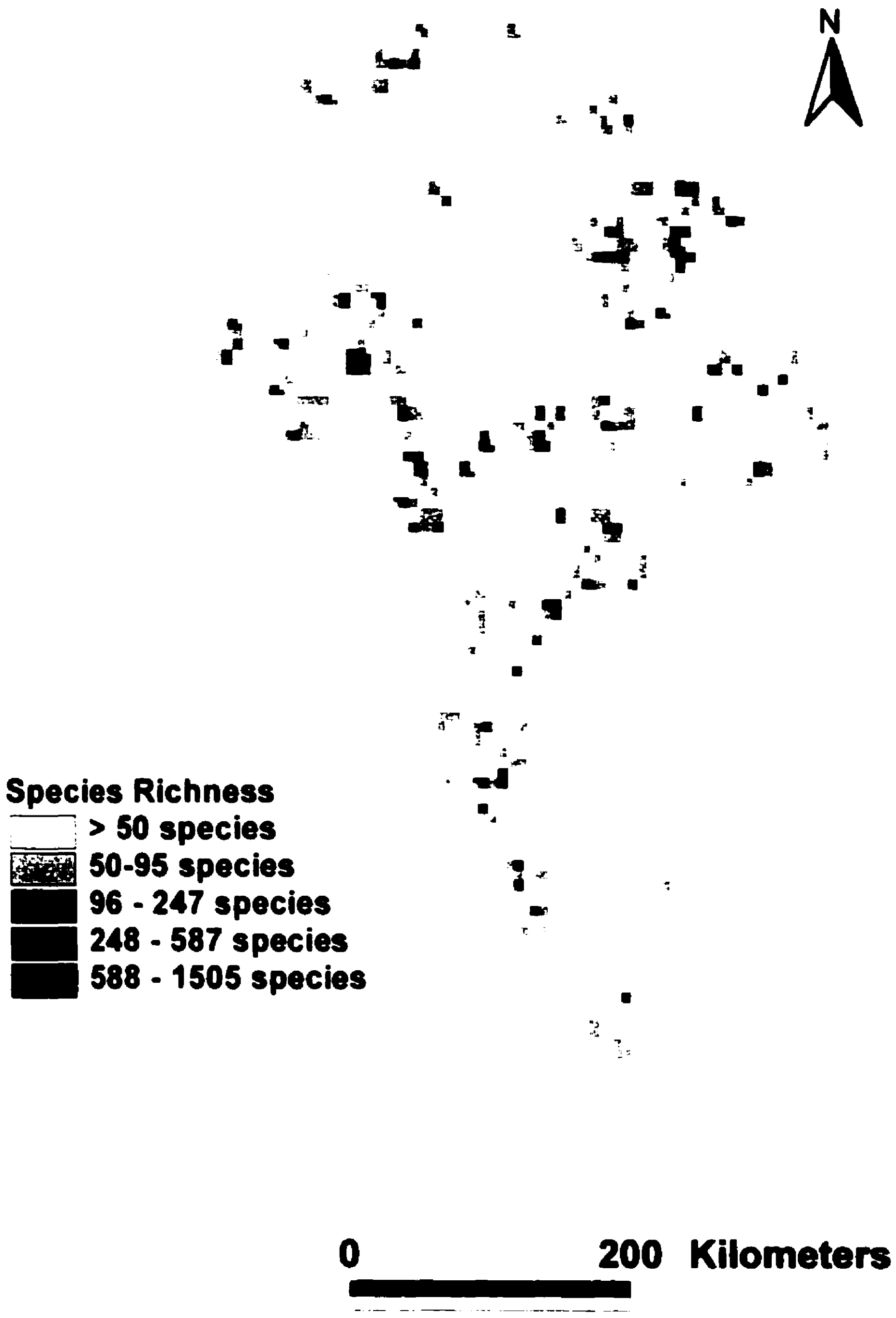
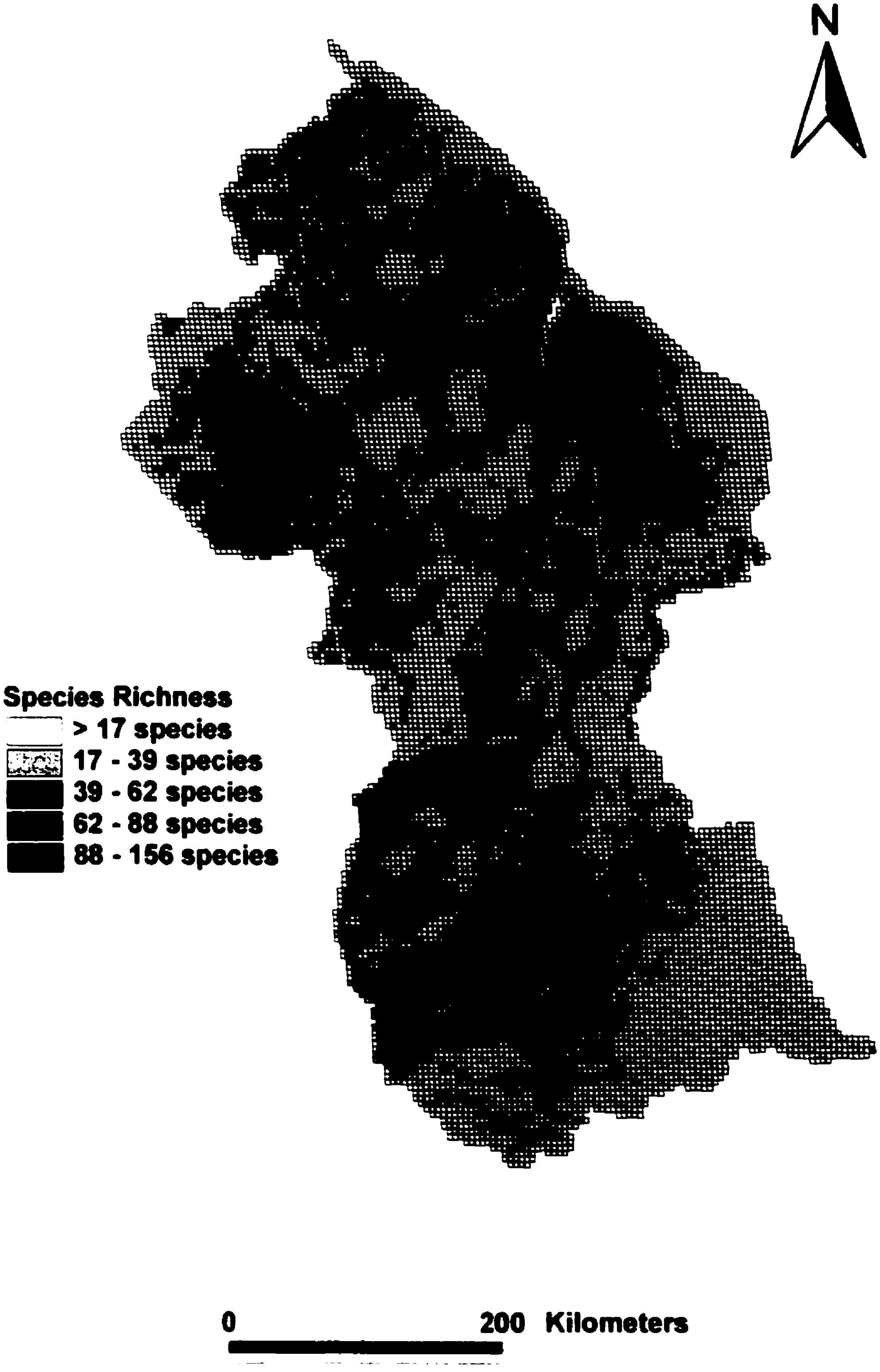


Figure 25: Species Richness using Dataset of 320 Species



5.3.2 Restricted Range Distribution

Restricted range values for species in the reduced dataset ranged from 0.0000298 – 0.000758 (Figure 26). As with species richness, a small number (in this case 0.29 %) of grid cells contained the most restricted species (restricted range value: 0.000650-0.000758), whereas the very widespread species (0.0000298-0.000108) accounted for 71 % of all grid cells. The sites with the most restricted species are clustered in the centre of Guyana, to the north of Kaieteur Falls, near Mahdia, Issano, Bartica and Ituni. Like species richness, there does not appear to be any gradient across the country. The spatial overlap of grid cells containing the most restricted species are not correlated with the most species-rich grid cells ($r^2 = 0.285$, $p > 0.5$).

5.3.3. Species Richness Hotspots

Species richness hotspots (top 5 % of species-rich grid cells) for all species are shown in Figure 27. The percent overlap calculated using the Jaccard coefficient between each of the 10 taxonomic group is shown in Table 8. There is a very low overlap (2 %) between the hotspots of all animal groups combined and all plant groups combined. The mean overlap between taxonomic groups was 9.8 % (range 0-78 %). Overlap in hotspots appears to be the highest between taxonomic groups that share the same ecological requirements such as ferns and melastomes (76 %), legumes and understorey trees (78%), and melastomes and orchids (40%). Clearly, these data provide little support for the notion that species-rich hotspots for one taxonomic group will coincide with species-rich hotspots for less-known taxa.

5.3.4 Restricted Range Hotspots

The restricted range hotspots (the top 5% of grid cells with the highest restricted range value) for all species is shown in Figure 28. Restricted range hotspots show

Figure 26: Restricted Range using Dataset of 320 Species

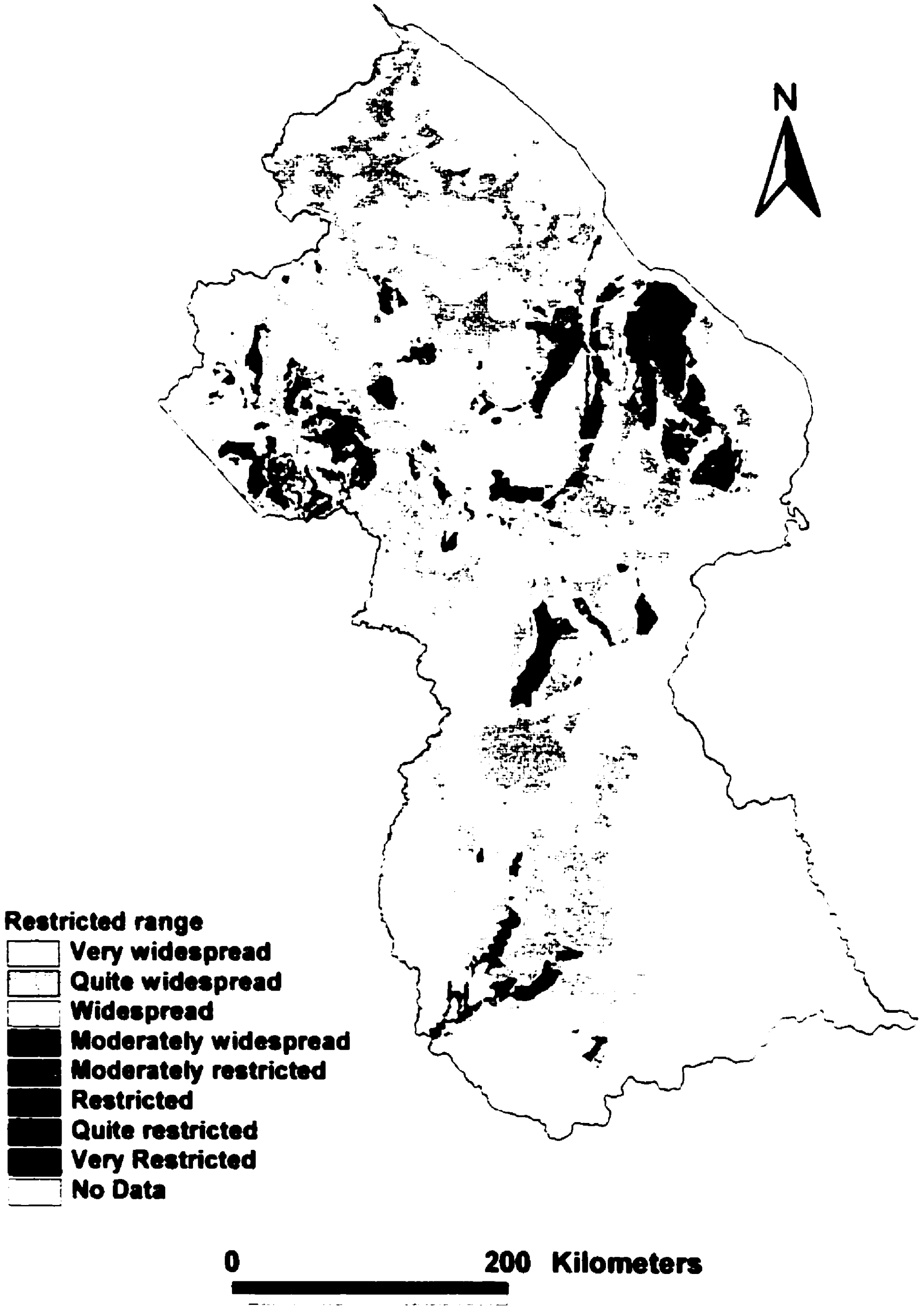


Figure 27: Species Richness Hotspots

Figure 28: Restricted Range Hotspots

Table 8 - Overlap of Species Richness Hotspots (n=number of grid cells in common)

<u>Richness</u>	**Birds**	**Understorey Trees**	**Ferns**	**Amphibians**	**Emergent Trees**	**Legumes**	**Mammals**	**Melastomes**	**Orchids**	**Sedges**	**All Plants**
Birds	-	0 %	0 %	24 % (n=219)	0 %	0 %	0 %	0 %	0 %	0 %	-
Understorey Trees		-	29 % (n=2805)	0 %	(n=436)	78 % (n=5675)	14 % (n=442)	16 % (n=262)	3 % (n=286)	37 % (n=4172)	-
Ferns			-	0 %	5 % (n=411)	28 % (n=2032)	0 %	76 % (n=1201)	27 % (n=2569)	8 % (n=767)	-
Amphibians				-	0 %	0 %	0 %	0 %	0 %	0 %	-
Emergent Trees					-	0 %	32 % (n=998)	9 % (n=139)	5 % (n=394)	0 %	-
Legumes						-	0 %	0 %	0 %	24 % (n=1736)	-
Mammals							-	0 %	0 %	0 %	-
Melastomes								-	40 % (n=627)	0 %	-
Orchids									-	0 %	-
Sedges										-	-
All Animals	-	-	-	-	-	-	-	-	-	-	2 % (n=102)

a slightly different trend than species richness hotspots (Table 9). The overall overlap between restricted range hotspots for plants and animals is 21 %. The mean overlap between taxonomic groups is 12.1 % (range 0.18 %- 63%). As with species richness hotspots, taxonomic groups that share similar ecological requirements have the highest degree of overlap: melastomes and orchids (63%), ferns and orchids (57%), understorey trees and legumes (54%), ferns and melastomes (50 %), and understorey trees and melastomes (43 %). Interestingly, the overlap between species-richness hotspots and restricted range hotspots was found to be quite high (mean of 71.4 %, range 50-100 %) (Table 10). This may indicate that certain species-rich areas in Guyana are also centers of endemism and that these areas have similar biogeographical features.

5.3.5 Irreplaceability Values

Summed irreplaceability maps (the sum of the irreplaceability values for all species considered) were produced using the reduced dataset for a target of 3 occurrences of each species (Figure 29).

5.3.6 Priority Biodiversity Site Selection

5.3.6.1 Species Richness

The priority biodiversity sites selected using species richness are shown in Figure 30. These sites represent the most species-rich sites in Guyana. The sites are located in or near Kaieteur Falls, Bartica, the Kanuku Mountains, and Georgetown.

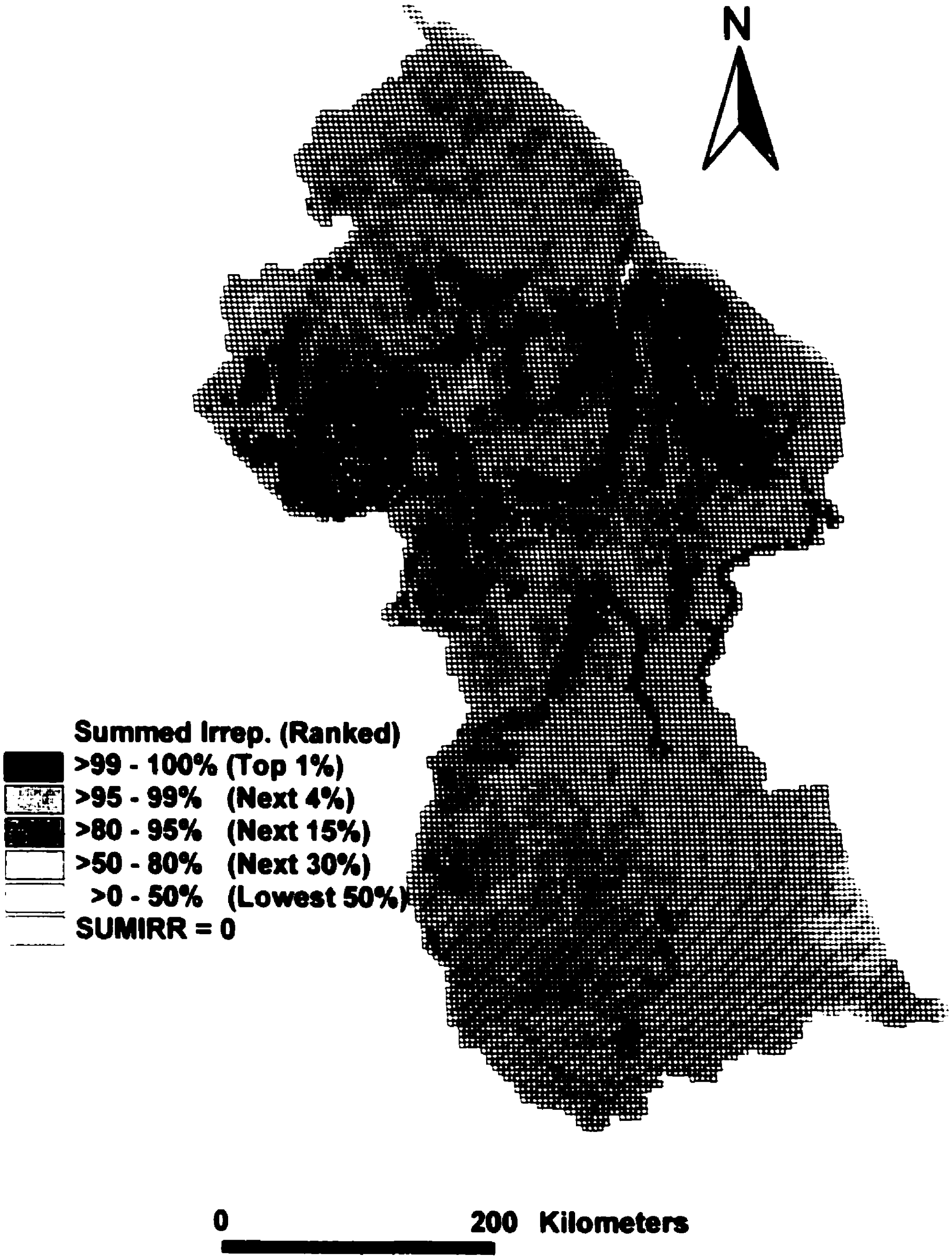
Table 9 - Overlap of Restricted Range Hotspots (n=number of grid cells in common)

Restricted Range	**Birds**	**Understorey Trees**	**Ferns**	**Amphibians**	**Emergent Trees**	**Legumes**	**Mammals**	**Melastomes**	**Orchids**	**Sedges**	**All Plants**
Birds	-	0 %	30 % (n=343)	2 % (n=219)	0 %	0 %	0 %	0 %	24 % (n=282)	0 %	-
Understorey Trees		-	15 % (n=1211)	0 %	7 % (n=300)	54 % (n=3421)	4 % (n=147)	43 % (n=702)	15 % (n=925)	26 % (n=1975)	-
Ferns			-	0 %	12 % (n=521)	17 % (n=1092)	0 %	50 % (n=811)	57 % (n=3484)	0.5 % (n=41)	-
Amphibians				-	0 %	0 %	0 %	0 %	0 %	0 %	-
Emergent Trees					-	0.18 % (n=8)	25 % (n=961)	39 % (n=637)	29 % (n=1252)	0 %	-
Legumes						-	0 %	0 %	16 % (n=1030)	17 % (n=1069)	-
Mammals							-	0 %	0 %	0 %	-
Melastomes								-	16 % (n=1033)	0 %	-
Orchids									-	0 %	-
Sedges										-	-
All Animals	-	-	-	-	-	-	-	-	-	-	21 % (n=1143)

Table 10 - Overlap of Species Richness and Restricted Range Hotspots (n=number of grid cells in common)

Hotspots	**Birds richness**	**Understorey Trees Richness**	**Ferns Richness**	**Amphibians Richness**	**Emergent Trees Richness**	**Legumes Richness**	**Mammals Richness**	**Melastomes Richness**	**Orchids Richness**	**Sedges Richness**
Birds Restricted	76 % (n=1172)									
Understorey Trees Restricted		75 % (n=6544)								
Ferns Restricted			59 % (n=4573)							
Amphibians Restricted				100 % (n=4573)						
Emergent Trees Restricted					63 % (n=2681)					
Legumes Restricted						60 % (n=3758)				
Mammals Restricted							82 % (n=3117)			
Melastomes Restricted								96 % (n=1561)		
Orchids Restricted									53 % (n=3291)	
Sedges Restricted										50 % (n=3828)

Figure 29: Summed Irreplaceability Target of 3 Occurrences



5.3.6.2 Summed Irreplaceability

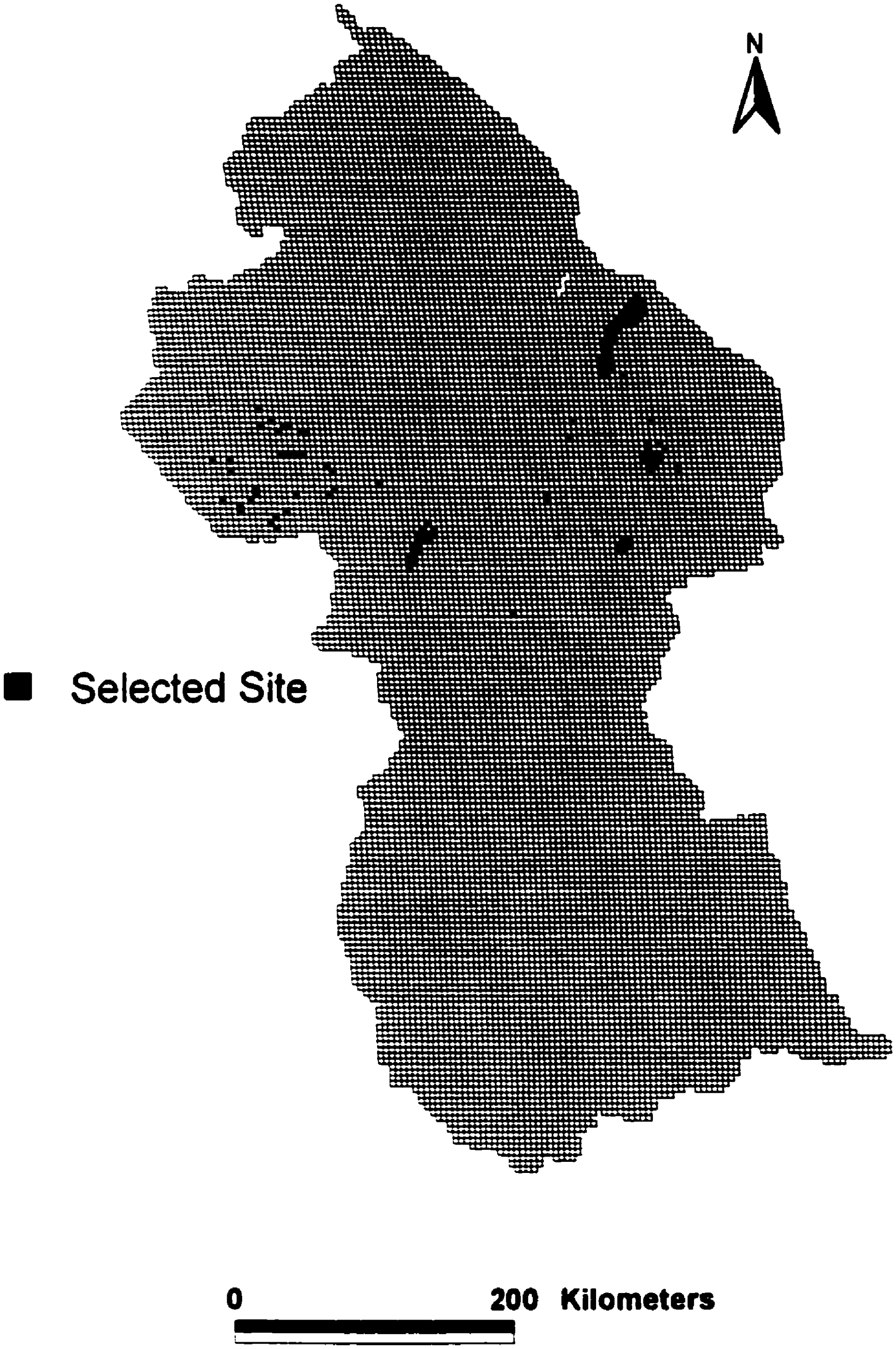
Priority biodiversity sites using irreplaceability were selected using a minimum set algorithm built from within C-Plan based the summed irreplaceability value for the reduced database. A target of 3 occurrences was used to derive the minimum set of sites (Figure 31). The priority biodiversity sites are more evenly distributed around the country than those based on species richness and include sites near Kaieteur Falls, the Pakaraima Mountains, the Kanuku Mountains, and Bartica. The degree of spatial overlap among minimum sets using species richness and irreplaceability, as assessed by the Jaccard coefficient, was only 17.8 %. The overlapping sites occurred near Kaieteur Falls, Bartica and near the Kanuku Mountains.

5.3.7 Cross-Taxon Surrogacy

Minimum sets of priority sites were also run for each of the ten taxonomic groups using summed irreplaceability with a target of 3 occurrences. To test the efficiency of the different taxonomic groups as surrogates for one another, species accumulation curves were examined. Species accumulation curves track the efficiency of the accumulation of each taxonomic group when priority sites are selected. In this case the optimum was defined as the target taxonomic group being used to select sites to best represent itself (e.g. data on birds was used to

Figure 30: Priority Biodiversity Sites Selected using Species Richness

Figure 31: Priority Biodiversity Sites Selected using Summed Irreplaceability



select priority sites for birds). The accumulation curves of species for the other taxonomic groups were recorded when sites were select using each target-group (Figures 32a-j). The species accumulation indices with confidence limits for each target taxon, each other taxon as a surrogate and the random curve are shown in Figure 33a-j. In all cases, summed irreplaceability was more effective in selecting priority sites to represent a specific target taxon than random. For all groups, the target-taxon and surrogate-taxonomic groups were more effective than random in selecting sites to represent a target taxon.

For birds, only amphibians were effective as a surrogate. The other groups were similar to each other in their effectiveness as surrogates and were more effective than random (Figure 33a). For understorey trees, none of the groups were very effective as surrogates, however birds, ferns and amphibians were marginally effective and all the other groups were more effective than random (Figure 33b). For ferns, only understorey trees were effective as a surrogate (Figure 33c). All other groups were similar in their effectiveness and were more effective than random. For amphibians, none of the groups were effective surrogates, however sedges, ferns, understorey trees, birds, mammals and legumes performed marginally better than the rest and all were more effective than random (Figure 33d). For emergent trees, none of the groups were effective as surrogates, however mammals were slightly better than the rest of the groups and they were all more effective than random (Figure 33e). For legumes, none of the groups were effective as surrogates, however sedges were marginally better than the rest and they were all more effective than random (Figure 33f). For mammals, none of the groups were effective surrogates, however amphibians were marginally better than the rest of the groups and all were more effective than random (Figure 33g). For melastomes, both ferns and understorey trees were effective surrogates. The rest of the groups were more effective than random (Figure 33h). For orchids, melastomes were effective surrogates and amphibians, understorey trees and ferns were marginally effective as surrogates. The rest of the groups were more effective than random (Figure 33i). Finally, for sedges, none of the groups were effective as surrogates, however they were all more effective than random (Figure 33j). Considering all target taxa, only 4 out of 10 taxonomic groups had effective surrogates and only one taxonomic group was effective as a surrogate in more than one case: understorey trees. Interestingly, when compared with the overlap of species richness hotspots, only 2 out of the 4 surrogate-target taxa pairs were similar – melastomes and ferns and orchids and melastomes. In Guyana, these taxonomic groups generally share similar ecological requirements. However, some groups with similar ecological requirements were not efficient surrogates.

5.3.8 Comparison with Environmental Domains and Vegetation Classes

The priority biodiversity sites selected using a minimum set algorithm with summed irreplaceability and a target of 3 occurrences of each environmental domain or vegetation type are shown in Chapter 3–Figure 19e-h. The accumulation of species for each of these minimum sets are shown in Figures 34 a-d. For all cases, the species in the reduced dataset were represented at least three times before all domains or vegetation classes could be represented 3 times. Thus, all of the species were represented three times in the sites selected before all of the domains or vegetation types could be represented. The percent of grid cells required to represent all species at least three times is presented in Table 11. The mean percent of grid cell required to represent all species for all four classifications was 48.8 %.

When the data for plant species in the reduced dataset were used to select priority biodiversity sites based on three occurences, only 15.8 % of the vegetation classes were captured (Figure 35). This is a very low amount considering the plant groups range from sedges and ferns to emergent trees found in the *Lecythidaceae* family.

Figure 32: (a) Species Accumulation Curves when Birds are the Target Group; (b) Species Accumulation Curves when Understorey Trees are the Target Group

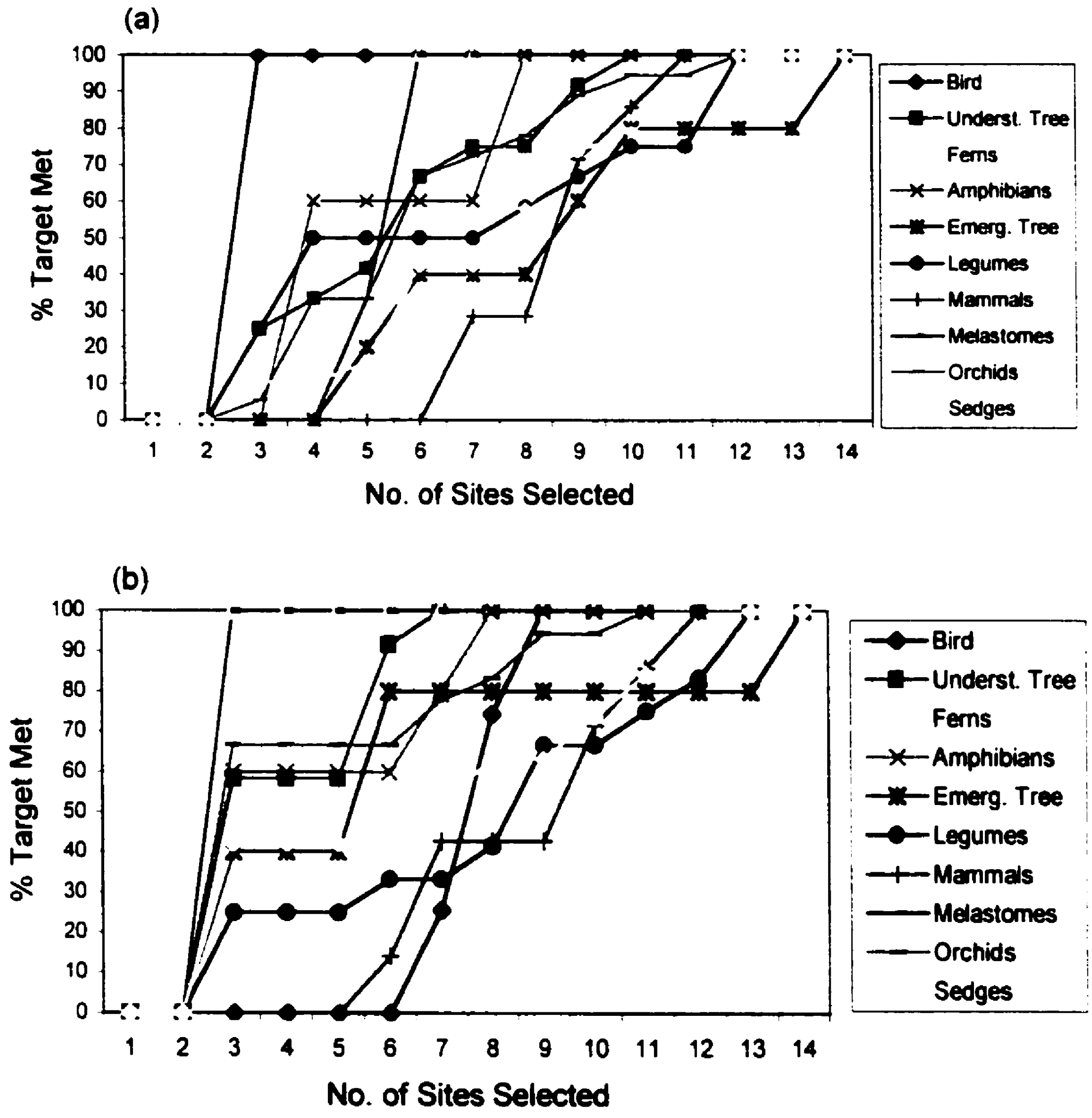


Figure 32: (c) Species Accumulation Curves when Ferns are the Target Group; (d) Species Accumulation Curves when Amphibians are the Target Group

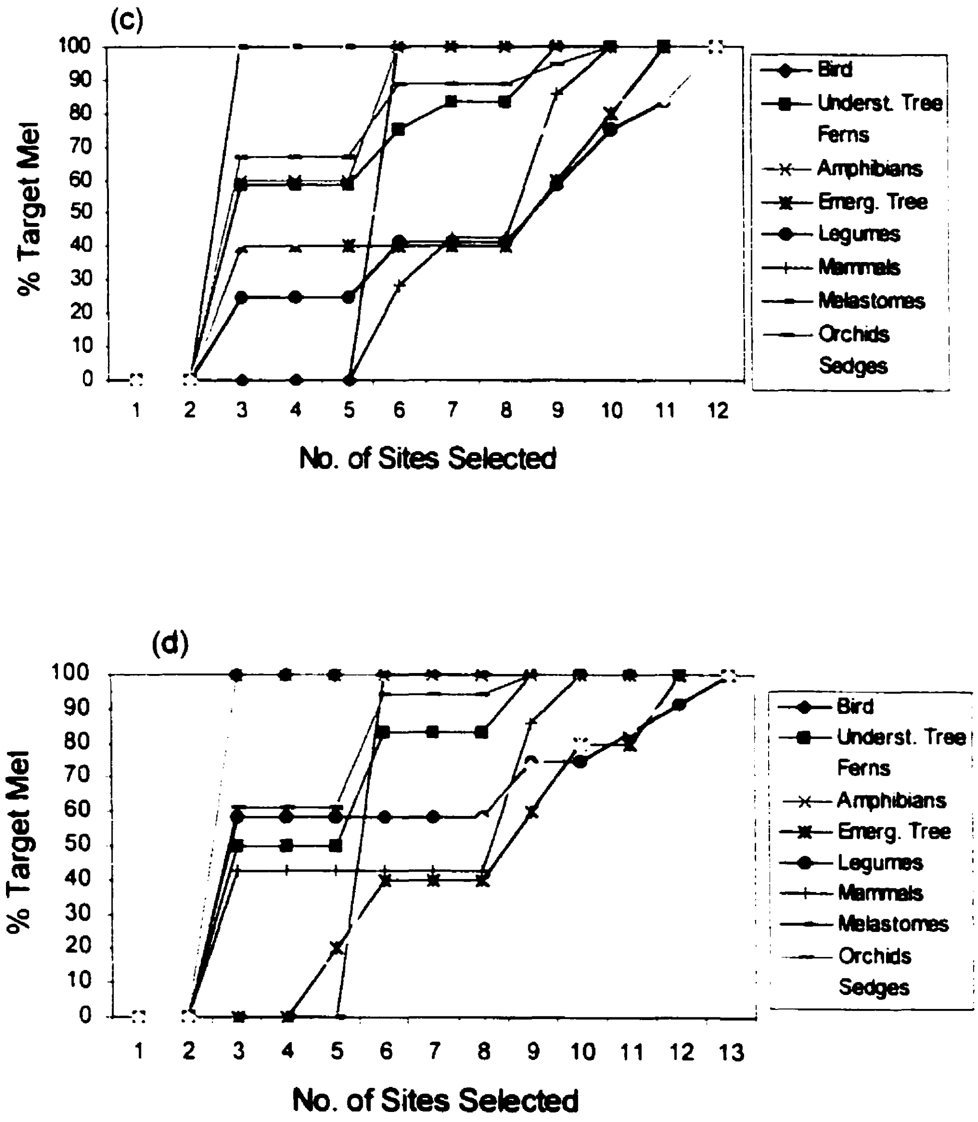
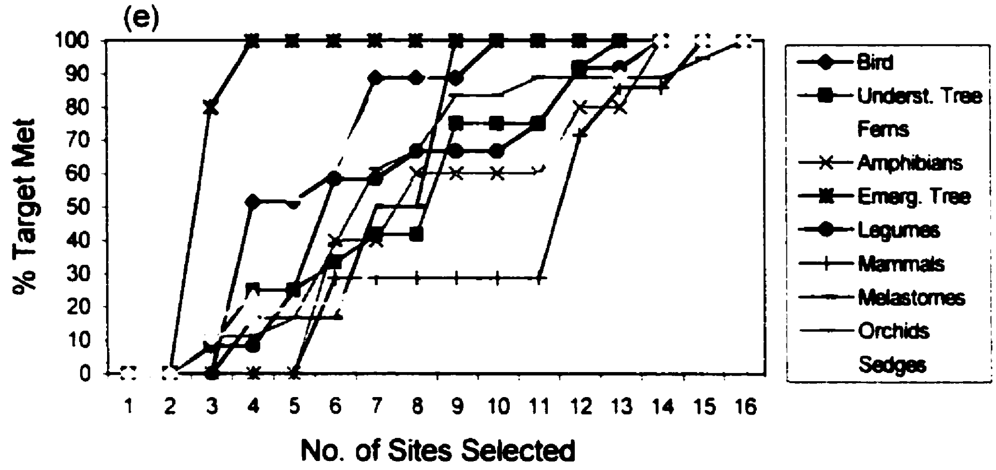


Figure 32: (e) Species Accumulation Curves when Emergent Trees are the Target Group; (f) Species Accumulation Curves when Legumes are the Target Group



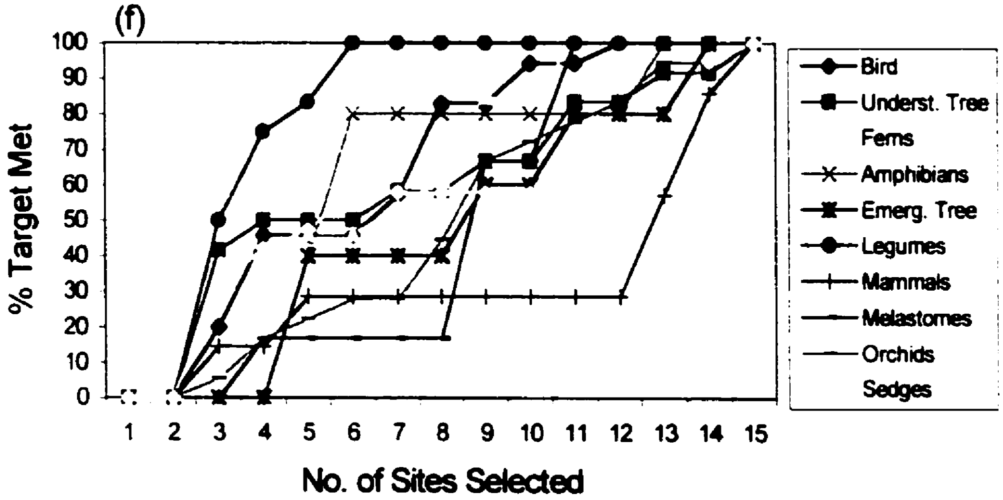


Figure 32: (g) Species Accumulation Curves when Mammals are the Target Group; (h) Species Accumulation Curves when Melastomes are the Target Group

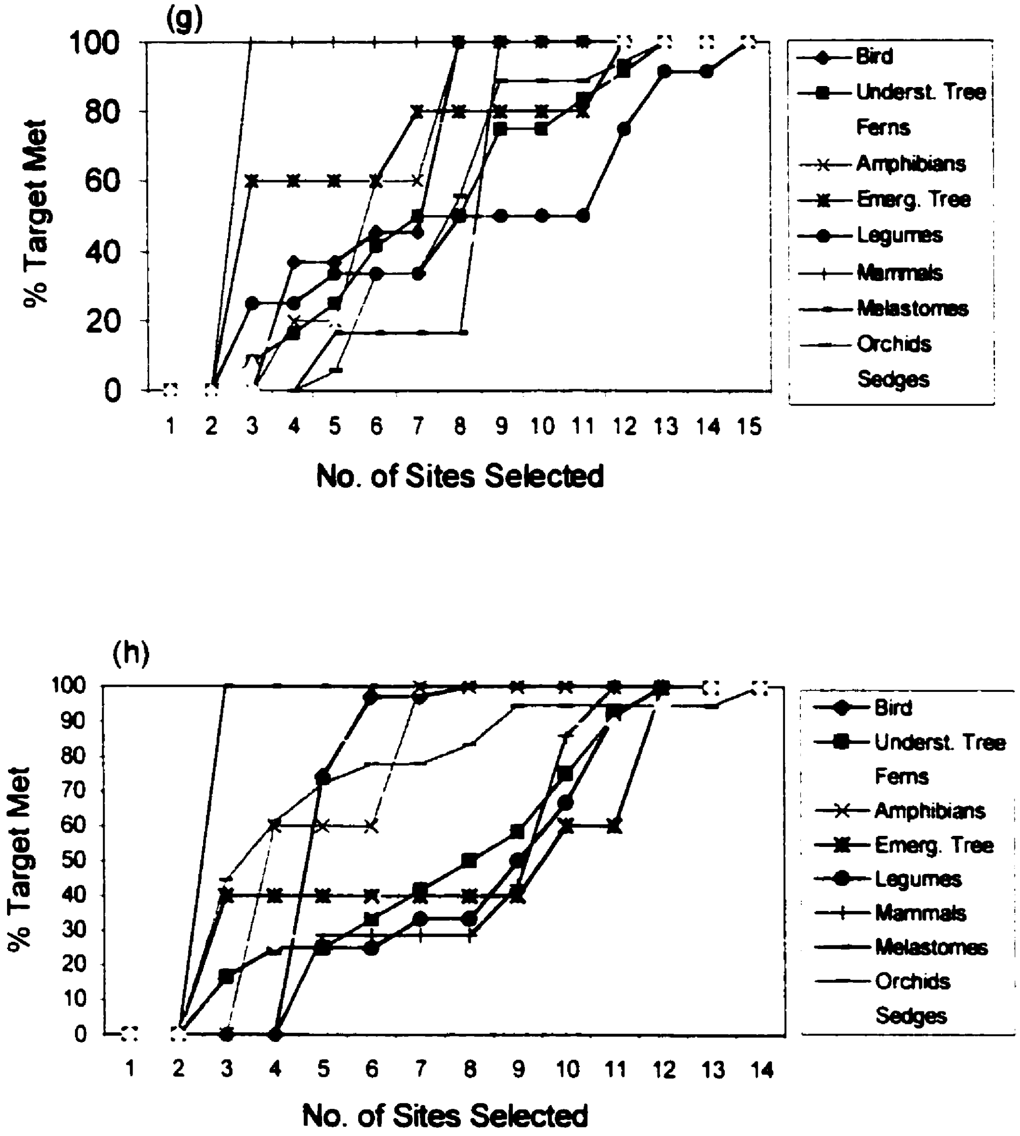
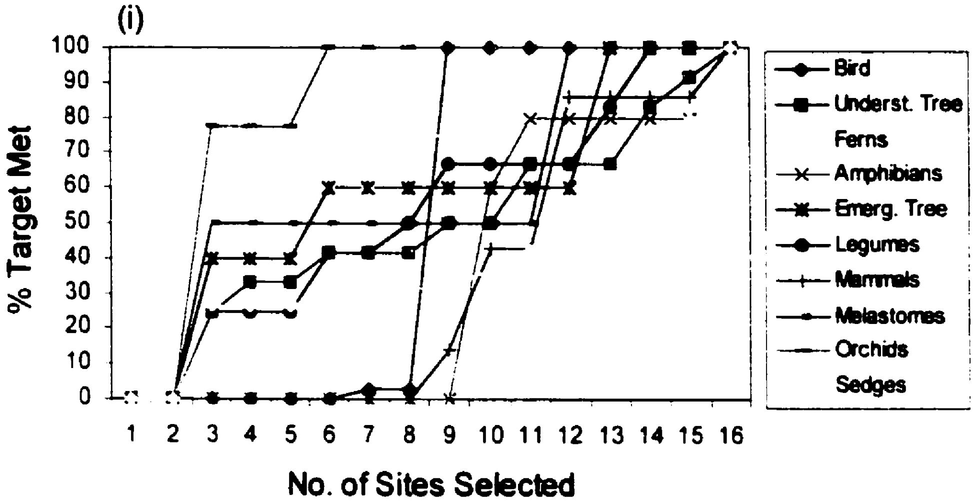


Figure 32: (i) Species Accumulation Curves when Orchids are the Target Group; (j) Species Accumulation Curves when Sedges are the Target Group



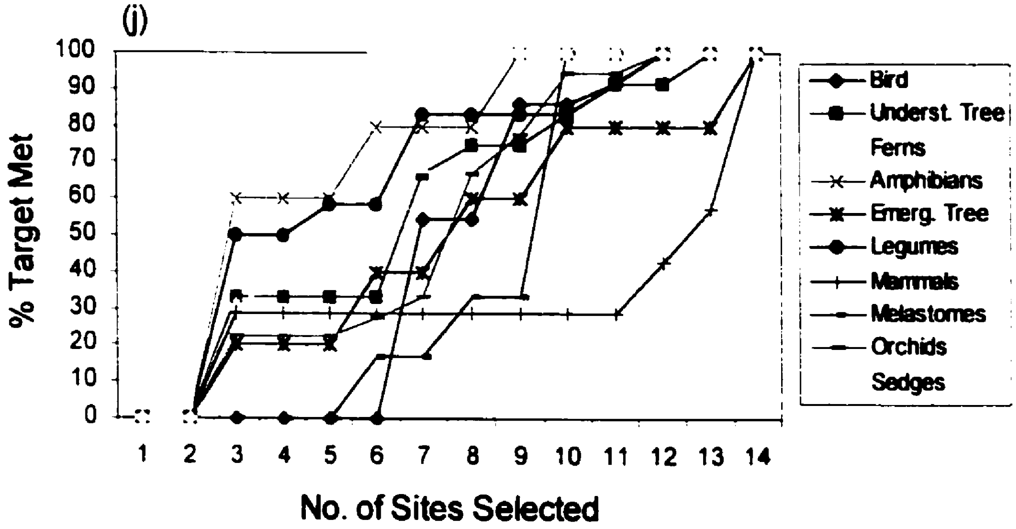


Figure 33: (a) Comparison of Areas when Birds are the Target Group; (b) Comparison of Areas when Understorey Trees are the Target Group

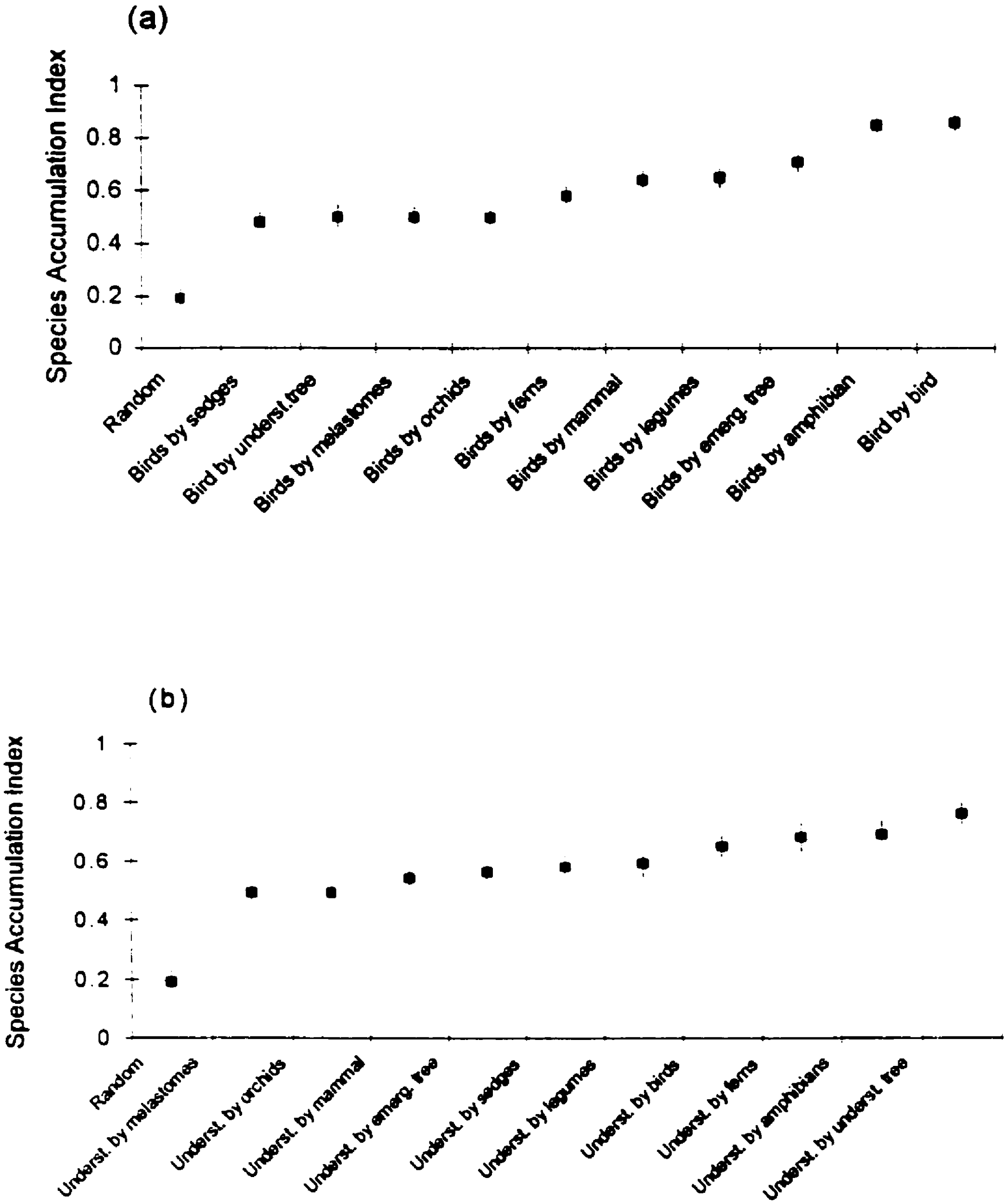
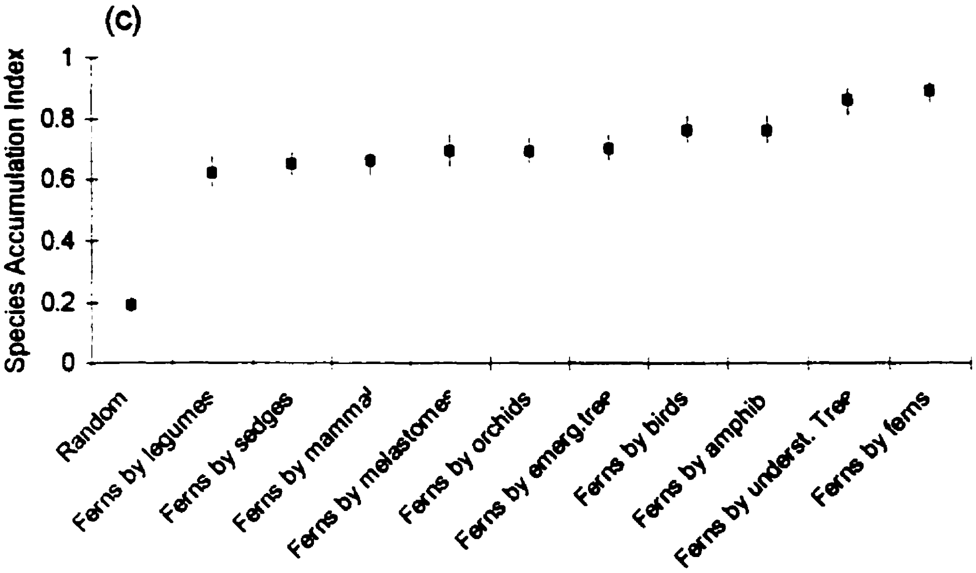


Figure 33: (c) Comparison of Areas when Ferns are the Target Group; (d) Comparison of Areas when Amphibians are the Target Group



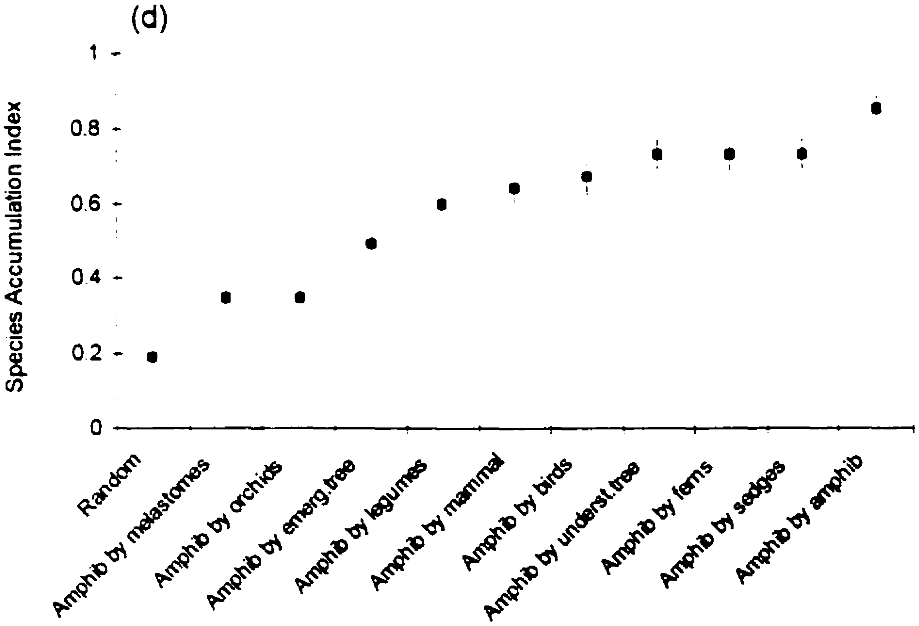


Figure 33: (e) Comparison of Areas when Emergent Trees are the Target Group; (f) Comparison of Areas when Legumes are the Target Group

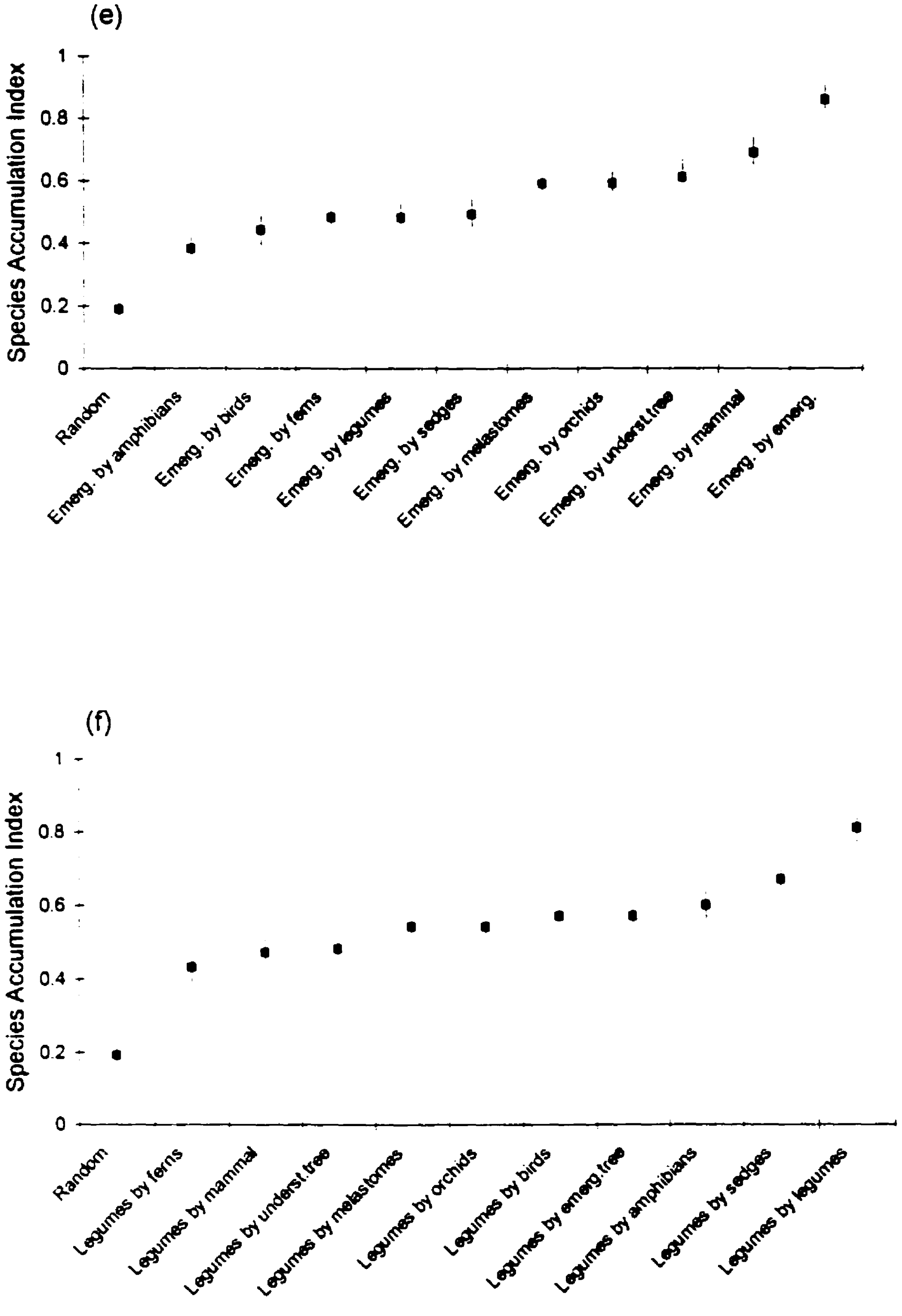


Figure 33: (g) Comparison of Areas when Mammals are the Target Group; (h) Comparison of Areas when Melastomes are the Target Group

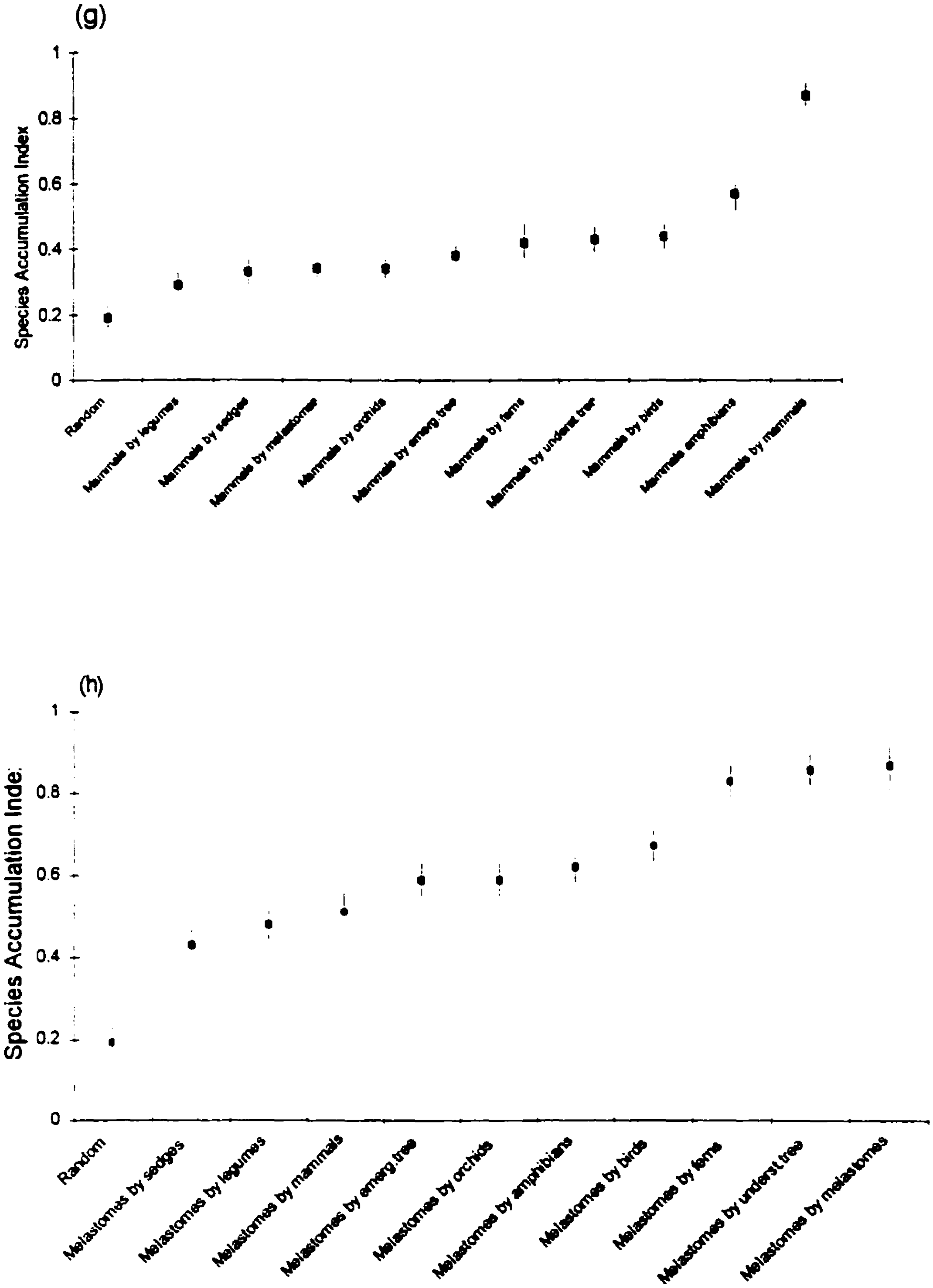


Figure 33: (i) Comparison of Areas when Orchids are the Target Group; (j) Comparison of Areas when Sedges are the Target Group

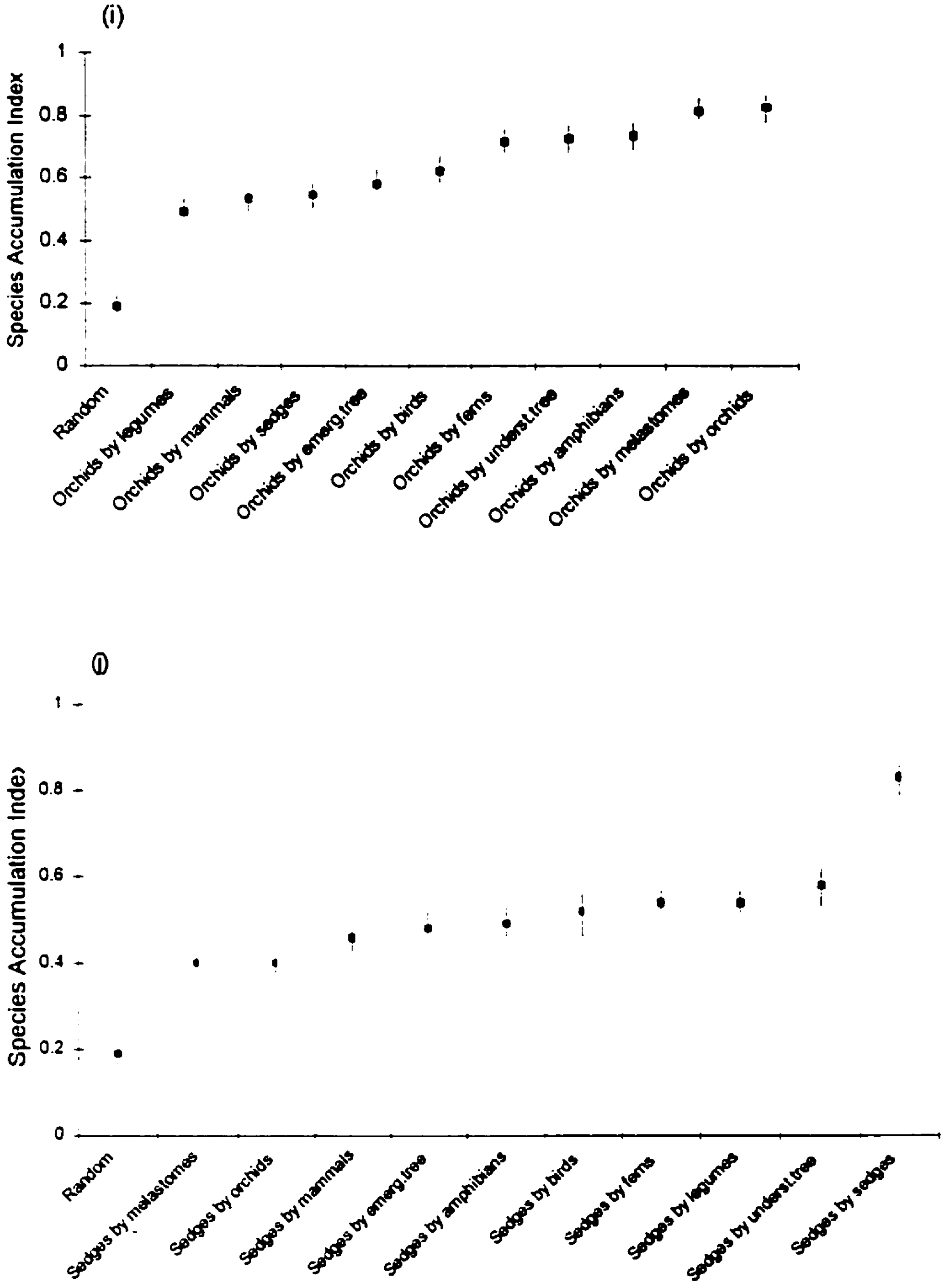


Figure 34: (a) Species Accumulation when 228 Domains are used to Select Priority Sites; (b) Species Accumulation when 100 Domains are used to Select Priority Sites

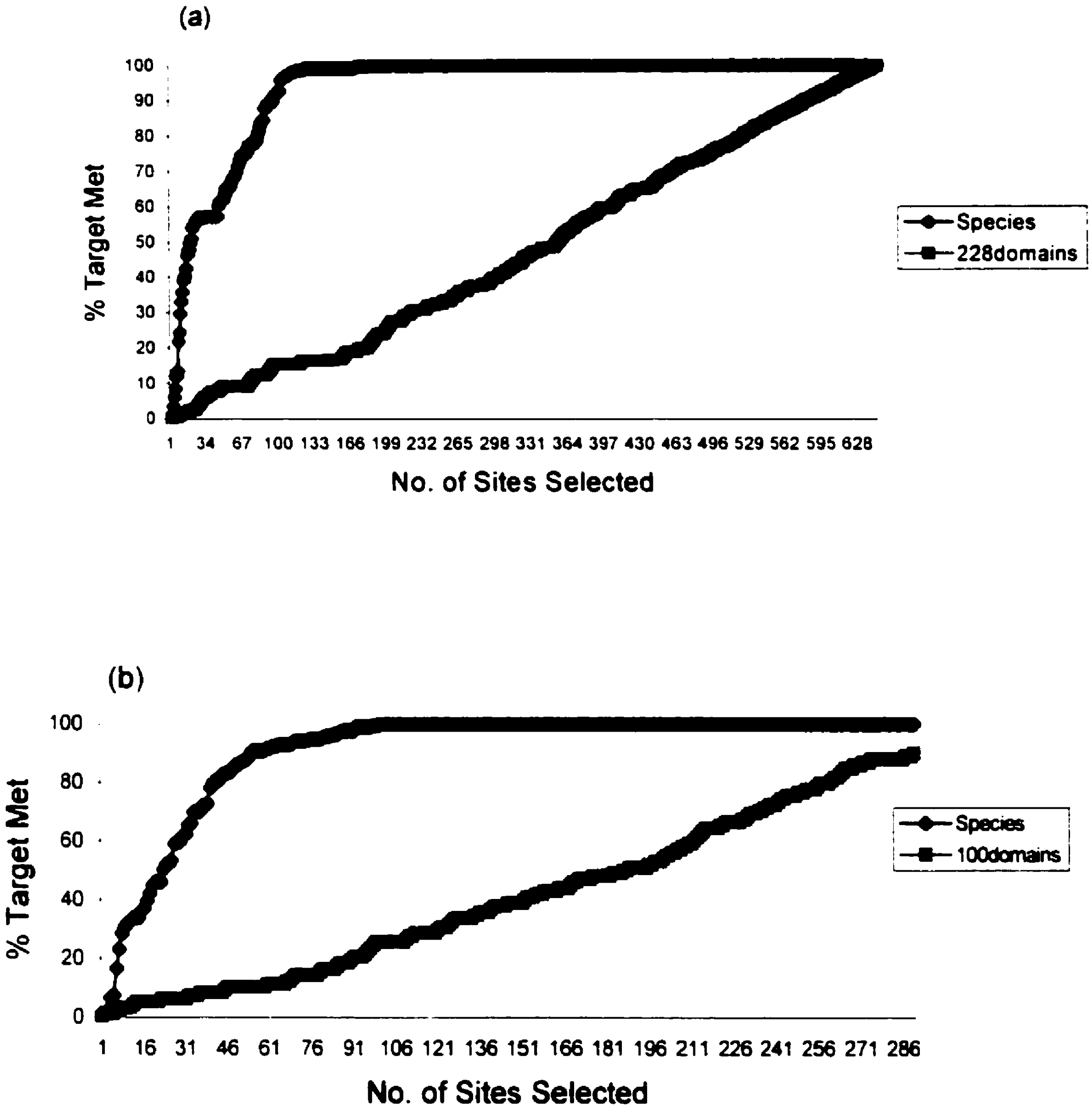
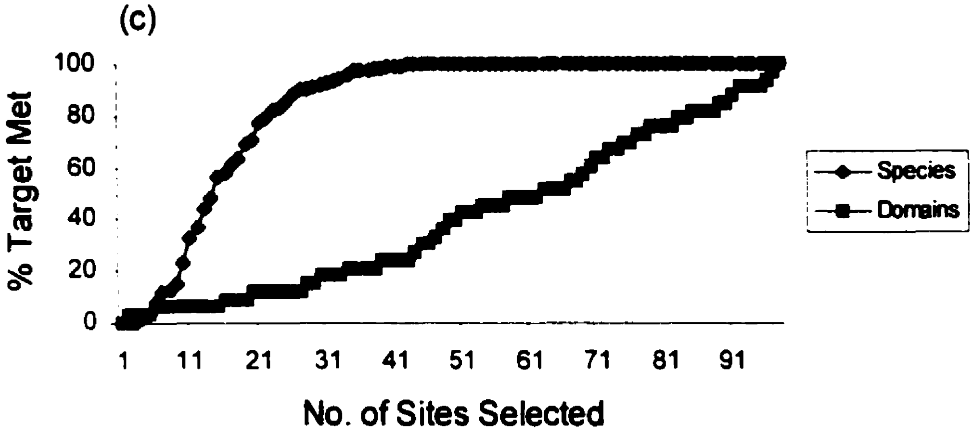


Figure 34: (c) Species Accumulation when 34 Domains are used to Select Priority Sites; (d) Species Accumulation when Vegetation Classes are used to Select Priority Sites



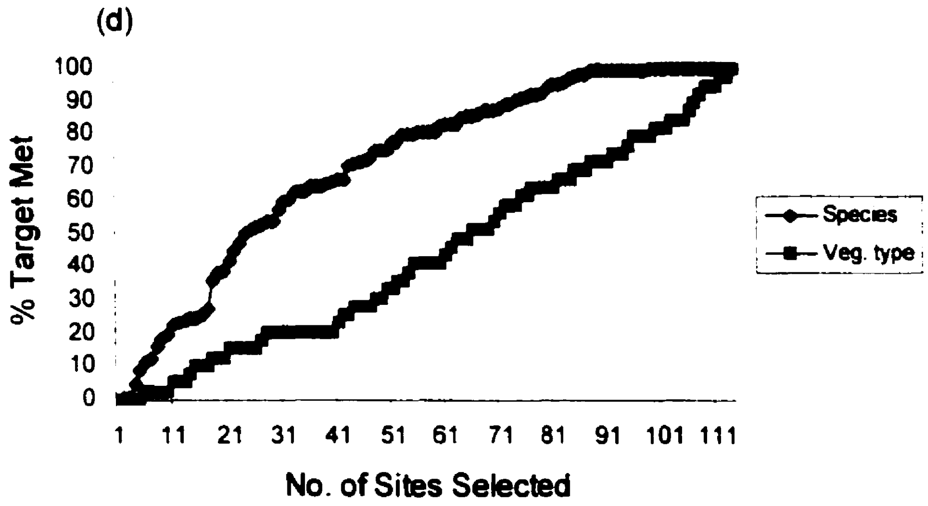


Figure 35: Accumulation of Vegetation Classes when Plants are used to Select Priority Sites

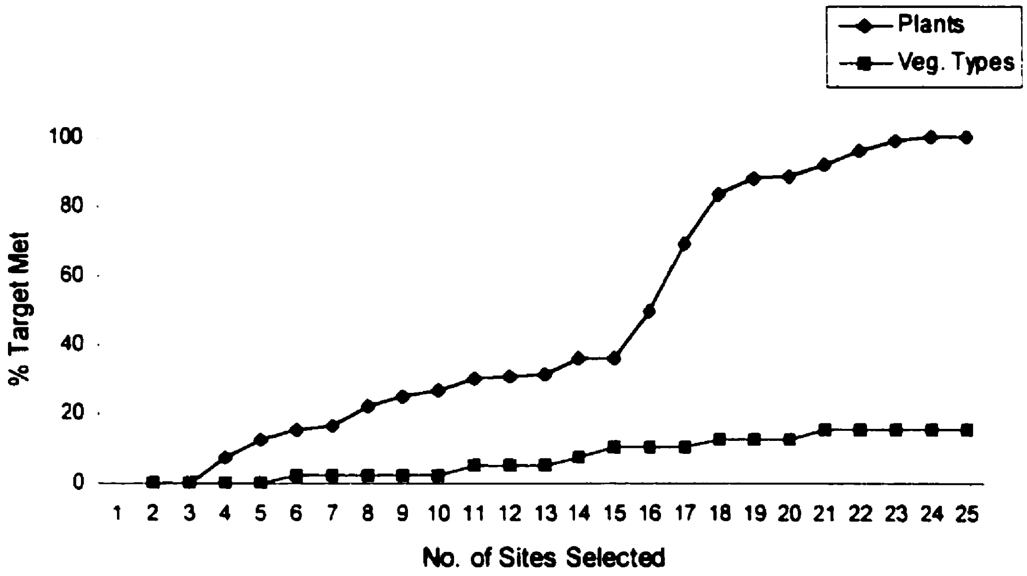


Table 11 - Percent of grid cells required to represent all species in the reduced dataset when priority sites were selected using environmental domains or vegetation classes

Classification	**No. of Sites Selected**	**% of grid cells required to represent all species**
34 Environmental Domains	98	45.9 %
100 Environmental Domains	290	34.8 %
228 Environmental Domains	646	28.1 %
Vegetation Classes	113	86.7 %

5.4. DISCUSSION

The results of this chapter demonstrate that selecting priority biodiversity sites for conservation planning is complex. Not only do different measures of biodiversity produce different results in terms of the location of priority biodiversity sites, but each taxonomic group can influence the overall pattern of biodiversity differently, resulting in very little overlap in priority sites between taxonomic groups. There are several instances where one taxonomic group acts effectively as a surrogate for another group, however these cases are the exception for both species richness and summed irreplaceability measures rather then the norm. The finding that there is very little correspondence at a selection unit size of 16 km^2 of richness sites for different taxonomic groups compares with other studies which have recently demonstrated the same result (Prendergast *et al.* 1993, Lombard *et al.* 1995, Dobson *et al.* 1997, Van Jaarsveld *et al.* 1998). When summed irreplaceability is used as a measure of species-complementarity, rarity and richness combined, the taxonomic groups chosen also showed poor cross-taxon congruence, except for a few groups. The lack of cross-taxon congruence however, is not enough to reject using the summed irreplaceability of several taxonomic groups to select priority biodiversity sites. In all instances, sites selected using one taxonomic group were effective at capturing a large portion of the species in the other taxonomic groups

(Figures 32 a-j). The efficiency of capturing those species may not have been sufficient (as measured by the area under the accumulation curves) to make them an effective surrogate in lieu of the actual taxonomic group, however when all species are used together to select priority sites, 40 % of species in all taxonomic groups are captured by the 7th site selected and this jumps to 60 % by the 10th site and 100 % by the 13th site (Figure 31). This clearly demonstrates the efficiency of this strategy.

The most species-rich sites were never the sites chosen in the minimum set of sites based on summed irreplaceability. This is largely due to the complementarity of sites chosen using summed irreplaceability to maximise the species. The species richness sites are clustered around areas of high species richness and do not necessarily represent all species in the reduced dataset. The summed irreplaceability sites are distributed throughout the country and represent all species in the reduced dataset at least 3 times. However, both were efficient in terms of the number of grid cells selected (23 for summed irreplaceability, 39 for species richness). This finding reinforces the idea recently published in the literature that the most species-rich sites are not necessarily the optimal sites for conservation (Flather *et al.* 1997, Howard *et al.* 1998, Van Jaarsveld *et al.*, 1998).

The number of species used in the reduced dataset was relatively low, however it represents the best dataset available for Guyana, and is comparable with most other similar studies (Prendergast *et al.* 1993, Scott *et al.* 1993, Curnutt *et al.* 1994, Williams *et al.* 1996, Lawton *et al.* 1998, Van Jaarsveld *et al.* 1998). Further studies will no doubt examine this issue.

A key finding of this study was the congruence when environmental domains were used. The majority of studies using systematic conservation planning tools have not attempted to look at the relationship between species and domains/vegetation classes. Results here demonstrated that the environmental domains and to a lesser extent vegetation classes were quite efficient at representing the species in the reduced dataset. On the one hand, this is encouraging for conservation planning as the use of environmental domains may be more feasible in countries where species data is lacking or poor. On the other hand, as discussed in the previous chapter, it suggests that more research is needed to determine how to divide abiotic environmental variables up into domains and vegetation classes.

This chapter demonstrates that there are many alternative combinations of sites which can be defined as priority biodiversity sites and which meet a specific representation target. One approach to deciding which is the "best" map to use for planning purposes may be to overlay all the maps and assume that it will yield the best representation of the known biodiversity in Guyana (Csuti and Kiester 1996). However, there are two inherent problems with this approach that will be examined in the next two chapters. First, the spatial scale at which the analysis was carried out ($16km^2$) may be too fine to be relevant to conservation planning. Using large grid cells to select priority sites may alter the selection of sites and the ability of certain taxonomic groups to act as effective surrogates. Secondly, the selection of grid cells in this chapter assumes that there are no "costs" to conserving biodiversity in Guyana. In reality, different sites of the country are more vulnerable to forestry and mining activities, thus an index of vulnerability must be applied to the selection of priority sites in order to determine in a real world context which sites will persist in the long term and retain biodiversity.

Chapter Six

Influence of Spatial Scale

6.1 INTRODUCTION

There are several aspects of spatial scale that are relevant to the selection of priority biodiversity sites. These include the extent, or size of the region in which an assessment is undertaken (Turner *et al.* 1989, Wiens 1989); the classification scale, or the scale at which features such as vegetation are defined; the grain, or smallest unit of observation within which the region is regarded as homogeneous (Turner *et al.* 1989, Wiens 1989); and the size of the selection unit (as per Pressey and Logan 1998). The first three aspects have been shown to influence measures of biodiversity pattern and hence, selection of priority biodiversity sites (Turner *et al.* 1989, Bedward *et al.* 1992, Stoms 1992, Pressey and Logan 1994, Stoms 1994). Of these four aspects, it is the size of selection units that is of particular importance for conservation planing. Selection units, defined here as the units of analysis used in systematic selection of priority biodiversity sites, are typically much larger than the grain of the data from which they are derived (Pressey and Logan 1998). However, when the underlying pattern of elements in the selection unit is integrated into a single value such as species richness, the distinction between selection unit and grain is blurred. Furthermore, most conservation decision-making evaluations use selection units that are different in size and configuration from the elements of biodiversity to be protected (Pressey and Logan 1998).

In systematic conservation planning, selection units are widely used and usually identified *a priori* to the selection of priority biodiversity sites (Pressey and Logan 1998). Selection units generally contain information on the occurrence, frequency and extent of species, environmental domains or vegetation classes, which is arranged in a manner that can be used in a systematic fashion. Typically, the size of the selection units used to determine priority biodiversity sites ranges from 1 km^2 to 640 km^2· and in many cases a regular grid is used (Margules and Nicholls 1988, Bedward *et al.* 1992, Pressey and Logan 1994, 1998, Lombard *et al.* 1999, Church *et al.* 1996, Williams *et al.* 1996, Van Jaarsveld *et al.* 1998, Howard *et al.* 1998, Erasmus *et al.* 1998, Wessel *et al.* 1999). A 1 km^2 grid selection unit may be too small a selection unit for most areas, as most protected area networks would include areas much larger than 1 km^2. On the other hand, using selection units that are too large may greatly reduce the efficiency by which the surrogates of biodiversity can be represented (Pressey and Logan 1998). The problem, which has been largely ignored in the literature, is that most systematic conservation planning approaches are trying to identify a set of minimum priority biodiversity sites that represent the known surrogate measures of biodiversity, and are trying to be as efficient as possible in terms of area, while still ensuring that the selection units selected are large enough alone or combined to be viable for the species or vegetation communities being assessed (Kirkpatrick 1983). Some studies, such as the GAP analysis in the United States, have chosen to work with relatively large selection units (approximately 640 km^2) to better represent patterns of gamma (or landscape) diversity (Csuti and Kiester 1996, Kietser *et al.* 1996).

To date, there is no strong theoretical basis for choosing the specific size of a selection unit. But, the literature suggests that the choice of selection units has important implications on the location of priority biodiversity sites. First, the size of the selection unit relative to the scale of the underlying feature such as a vegetation class, is important. Units that are too large may mask fragments of vegetation, while units that are too small may overestimate coarse-scale mapping (Pressey and Logan 1998). Second, different sizes of selection units may lead to different configurations of sites. For instance, for two areas in Idaho the patterns of species richness appeared to be sensitive to the size of the selection unit and there was no predicability in the patterns found from one size of selection units to the next (Stoms 1994). Thirdly, the efficiency of representation of surrogates of biodiversity is directly related to selection unit size. Pressey and Logan (1998) recently showed that the efficiency with which species or domains could be represented in priority biodiversity sites was higher for smaller selection units. Larger units however, showed an over-representation of many features that may in the long-term be beneficial. Lastly, an issue that becomes relevant when systematic conservation planning approaches are implemented on the ground, is the appropriateness of the selection unit for management purposes.

The development of hierarchy theory over the past several decades has brought forth the incorporation of scale and the notion of hierarchy into conservation planning (O'Neill 1996). One hypothesis that has emerged from hierarchy theory concerns the scales of pattern in space. The theory predicts that patterns change with an increase from one level of scale to another, and hence a distinct level of scale should show a distinct pattern (O'Neill 1996). Several tests of this hypothesis have been conducted (O'Neill *et al.* 1991, Levin 1992). These tests have found that with each level of scale there exists a distinct pattern that cannot be predicted from the previous level of scale (O'Neill 1996). If this holds true for measuring biodiversity, then the scale at which species and other surrogate measures of biodiversity are examined must be carefully considered each time that this information is used in decision-making processes.

This chapter uses the data presented in chapter 5 to examine the influence of selection unit sizes on: a) the observed spatial patterns of species richness; b) the efficiency of representing known species; c) the overlap in the location of high priority biodiversity sites from one selection unit level to another; and d) the influence the selection unit has on the ability of indicator taxa to act as surrogates for one another. There have been several studies recently addressing these issues (Davis and Stoms 1996, Erasmus *et al.* 1998, Pressey and Logan 1998), however none of them has systematically altered the selection unit size and examined the influence of selection unit size on the number, location and efficiency of priority biodiversity sites. Understanding the effects of scale by comparing the results from different selection units using the same data is crucial in beginning to address the likely trade-offs at different scales. Unlike other studies, this study does not assume a single value of species richness for each selection unit. Individual species distributions (recorded and predicted) are used at each level of selection unit size to avoid some of the problems of using data derived from the initial grain.

6.1.1 Species Richness

In a recent review on gaps in conservation networks, Flather *et al.* (1997) reviewed several published studies on species richness hotspots to try to determine whether among these studies there was any trend to suggest " a most appropriate scale" for conservation planning. They reviewed continental-scale, regional- and local-scale studies on the coincidence of species hotspots, and concluded that the continental-scale patterns of taxonomic overlap of species hotspots did not hold up at a regional–scale nor at a fine geographic scale for data across North America. Flather *et al.* (1997) only reviewed published data and were not able to vary the scale of investigation to test whether the same data measured at different scales, demonstrated similar patterns.

The first study to examine the scale dependency of species richness maps was conducted as part of the Idaho GAP Analysis Project (Stoms 1994). The study clearly showed that the observed spatial scale was very important in assessing species richness in an area. Stoms compared the species richness maps for two areas of Idaho at different spatial scales from 1000 ha to 1,000,000 ha. He concluded that in the case of Idaho, the variability of species richness decreased with increasing size of spatial sampling unit (*i.e.* from 1,000 ha to 1,000,000 ha), however there was no optimal scale at which to measure species richness. Rather, he showed that the question of optimal and appropriate scale cannot be provided by simple rules and that the appropriate scale to measure species richness may vary by ecoregion.

Since the size of selection units varies so much in studies and reports on species richness, it is difficult to compare the results of one study to another. Species richness is clearly dependent upon the resolution at which it is measured (Allen and Starr 1982). One of the ways to investigate how species richness varies with selection unit size and the implication this may have on selection of priority biodiversity sites, is to systematically vary the size of the unit and compare the location of priority sites at each new unit size. This approach is adopted in this chapter and used to investigate the influence of spatial scale.

6.1.2 Efficiency and Overlap of Selection Units

In an initial paper, Pressey and Logan (1995) looked at the effects of selection unit size of the selection of land classes in New South Wales, Australia. They found that smaller selection units were more efficient than larger ones at representing the conservation target of each land class. In a follow-up paper (Pressey and Logan 1998), they extend their analyses to try and address the reasons why smaller units were more efficient. They concluded that the larger units were usually representing land classes at above-target levels (*i.e.* over-representing certain land classes when a set conservation target was assigned). Although smaller units were more efficient, these units were generally too small to be viable protected areas (*i.e.* they were less than 10,000 ha. in size). Thus, a trade-off in efficiency may be necessary to achieve a realistic conservation target.

Davis and Stoms (1996) used data from Church *et al.* (1996) collected in 7.5 minute quadrangle in California, USA to examine the influence of selection unit size. Davis and Stoms (1996) aggregated species list for 7.5, 15 and 30 minute quadrates for an area of south-western California and selected priority sites using a maximal covering location problem model (an optimising technique) to select sites. They then compared species accumulations by site and the number of units required to represent all species. Davis and Stoms (1996) found that twelve (out of a possible 281) 7.5' quadrangles totalling 192 km^2 in size were required to cover all 333 vertebrate species, versus nine 15'quadrangles of 576 km^2 in total size and eight 30'quadrangles totalling 2,048 km^2. However, the location of the selection units at all three spatial scales required to represent the species was very similar. Davis and Stoms (1996) concluded that for southern California, the geographical location of priority biodiversity sites may be insensitive to the size of the selection unit due to the spatial autocorrelation of vertebrate assemblages, but the efficiency of capturing species, as with Pressey and Logan (1998), diminishes as the size of the selection unit increases (Davis and Stoms 1996).

6.1.3 Cross-Taxon Surrogacy

As reported in the previous chapter, there are several studies that report a limited concordance in patterns of high species richness between taxonomic groups, including this study. One of the few studies that examined the relationship in cross-taxon congruency and spatial scale, observed that the magnitude of the congruency varied greatly with scale (Murphy and Wilcox 1986, Murphy 1989). Murphy and Wilcox (1986) found the correlation between birds and butterflies in Great Britain was weak at a coarse biogeographic scale, stronger at the scale of riparian canyons and showed no relation at a scale of 1 ha plots. No study since Murphy and Wilcox (1986) has reviewed this problem or added data from tropical countries that is now available (see Howard *et al.* 1998 and Van Jaarsveld *et al.* 1998). This chapter examines the congruency of different taxonomic groups by looking at how well different taxonomic groups act as surrogates for other groups in the selection of priority biodiversity sites.

6.2 METHODS

In chapter 5, the reduced dataset of 320 species was used at a spatial scale of 16 km^2 to select priority biodiversity sites. In this chapter, the same reduced dataset was used to select priority biodiversity sites, however the spatial scale of the selection unit was altered to examine the effects of the size of the selection unit on species richness and priority biodiversity sites. To examine these effects, a 1 km x 1 km grid of Guyana was iteratively aggregated two by two to create six levels of units: 16 km^2 (13, 751 grid cells across Guyana), 64 km^2 (3,553 grid cells), 256 km^2 (942 grid cells), 1,024 km^2 (258 grid cells), 4,096 km^2 (77 grid cells) and 16,384 km^2 (25 grid cells).

6.2.1 Species Richness

The spatial distribution (recorded and predicted) of each species was overlaid on the 1 km by 1 km grid map of Guyana and the grid cells were iteratively aggregated 2 x 2 in ArcView (version 3.1, ESRI 1998) to create the six levels of units described above. The distribution of each species was overlaid on the new grid size. Species richness was calculated for each of the different size selection units by overlaying the maps of each species using a Boolean union and tallying the number of species in each grid cell. Species richness maps were produced for each level of selection units and were compared visually. The coefficient of variation of species richness (CV) was used to compare across levels after Stoms (1994). Data were normalised ($\log_{10}$) for each level of selection units. Additionally, for each level of selection units the number of species accumulated was calculated against the total area required to capture all species. Species accumulation curves were compared for each level of selection unit and for the 10 taxonomic groups identified in Chapter 5.

6.2.2 Selection of Priority Biodiversity Sites

Priority biodiversity sites were selected for each of the six levels of selection units using C-Plan (NSW NPWS 1999). Summed irreplaceability values were calculated for each grid cell at each level. A minimum set algorithm as described in the previous chapter was run for each of the 6 levels of selection units. The grid cell with the highest summed irreplaceability was selected first, the summed irreplaceability was re-calculated and then next highest summed irreplaceability grid was selected until all species were captured at least three times. The efficiency of representing each species at least 3 times was measured using an efficiency index (after Erasmus *et al.* 1998) where Efficiency $(E) = 1-x/t$ where x was the number of grid cells selected and t was the total number of grid cells that contained data. Minimum sets at each of the six levels were compared visually. However, since there are several possible solutions to representing each species at least 3 times (grid cells which are not totally irreplaceable can be exchanged), species accumulation curves and the number of grid cells needed to represent all species at least 3 times were compared for each of the six levels.

6.2.3 Cross-Taxon Surrogacy

The efficiency of taxonomic groups as surrogates for each other was investigated in the same manner as in Chapter 5, however the size of the selection unit was varied for each level. A minimum set of grid cells was derived in C-Plan (NWS NPWS 1999) using a protected area selection algorithm based on summed irreplaceability. A separate algorithm was run for each taxonomic group. A stopping rule of 3 occurrence was used however, in this case it was only applied to the taxonomic group (target-group) in question. The percent of species captured for all the other taxonomic groups was then measured. The resulting species accumulation curves were plotted, including a random curve generated from 1000 random runs, and used to examine the efficiency of groups to act as surrogates for each other. The area under each curve was calculated and plotted. Confidence limits (97.5 % - 2.5 %) were derived using a bootstrapping technique which ran 1000 replacement run for each combination.

6.3 RESULTS

6.3.1 Species Richness

Maps of the species richness at the different levels of selection units are presented in Figures 36 a-f. The maps provide a visual interpretation of the patterns across the different levels of selection units. The maximum species richness ranges from 156 species for the 16 km^2 grid cells to 312 for the 16,384 km^2 sized grid cells. When species richness is mapped across the levels, the patterns look reasonable consistent from one level at the 16 km^2 to 256 km^2 levels, with the most species in the middle section of Guyana (Pakaraima Mountains and area around Kaieteur Falls and Bartica/Georgetown). However, the very fine patterns of richness at 16 km^2 practically disappear by 256 km^2. At the larger selection unit sizes, the patterns are very inconsistent. At 16,384 km ^{2} grid cell size, the central lowland forests and the Pakaraima Mountains are still the richest areas, however the distinction of species-rich and species-poor areas within those regions becomes difficult. Figure 37 shows the relationship of variability in richness to the selection unit size as a log-log plot. The coefficient of variation (CV) of richness decreases rapidly from 16 km^2 to 256 km^2. At 256 km^2, the CV of richness stabilises and remains basically unchanged for the remaining 3 selection unit sizes (Figure 37). The maximum variability in richness is found at the 16 km^2 level and variability decreases substantially as the selection unit is increased. The between unit variability is lowest from 4,096 km^2 and larger. At these levels of selection units, each unit contains a similar mix of habitats and vegetation types.

6.3.2. Selection of Priority Biodiversity Sites

The maps of the priority biodiversity sites at each level are presented in Figures 38 a-f. There is very little overlap in the location of sites selected using the highest summed irreplaceability values. Some of the difference may be attributed to grid cells that have a lower summed irreplaceability value and are exchangeable with other sites with the same values. However, at the finer levels of size (16 km^2 - 256 km^2) there is a similar spread of sites across Guyana. The percent of grid cells required to represent each species in the reduced database 3 times varied from 0.16 %-32 % (Table 12). The number of grid cells required was relatively low, with the exception of 16,384 km^2 grid cell level, which required 32% of the available grids. Similarly, the efficiency of capturing each species 3 times in the grid cells varied from 0.68 – 0.99 (Table 12). These results indicate that at most of the levels, relatively little land is required to capture a representative sample of the biodiversity in Guyana, however the actual area of land varied from 344 km^2 - 68,800 km^2, a difference of 200 times. At 16,384 km^2, eight grid cells are required, which constitutes 32 % of the land. This much land is required, as several of the more rare species appear to have restricted ranges outside the most species-rich grid cells.

Table 12 – The percent of grid cells required to represent species and index of efficiency for different selection unit sizes (most efficient =1)

Selection Unit Size	**% of Grid Cells Required**	**Amount of Land Area**	**Efficiency Index**
16 km^2	0.16	344 km^2	0.99
64 km^2	0.47	1,010 km	0.98
256 km^2	1.38	2,967 km	0.98
1,024 km^2	2.7	5,805 km	0.97
4,096 km^2	7.8	16,770 km	0.92
16,384 km^2	32	68,800 km	0.68

Figure 36a: Species Richness at a Grid Size of 16 km^2

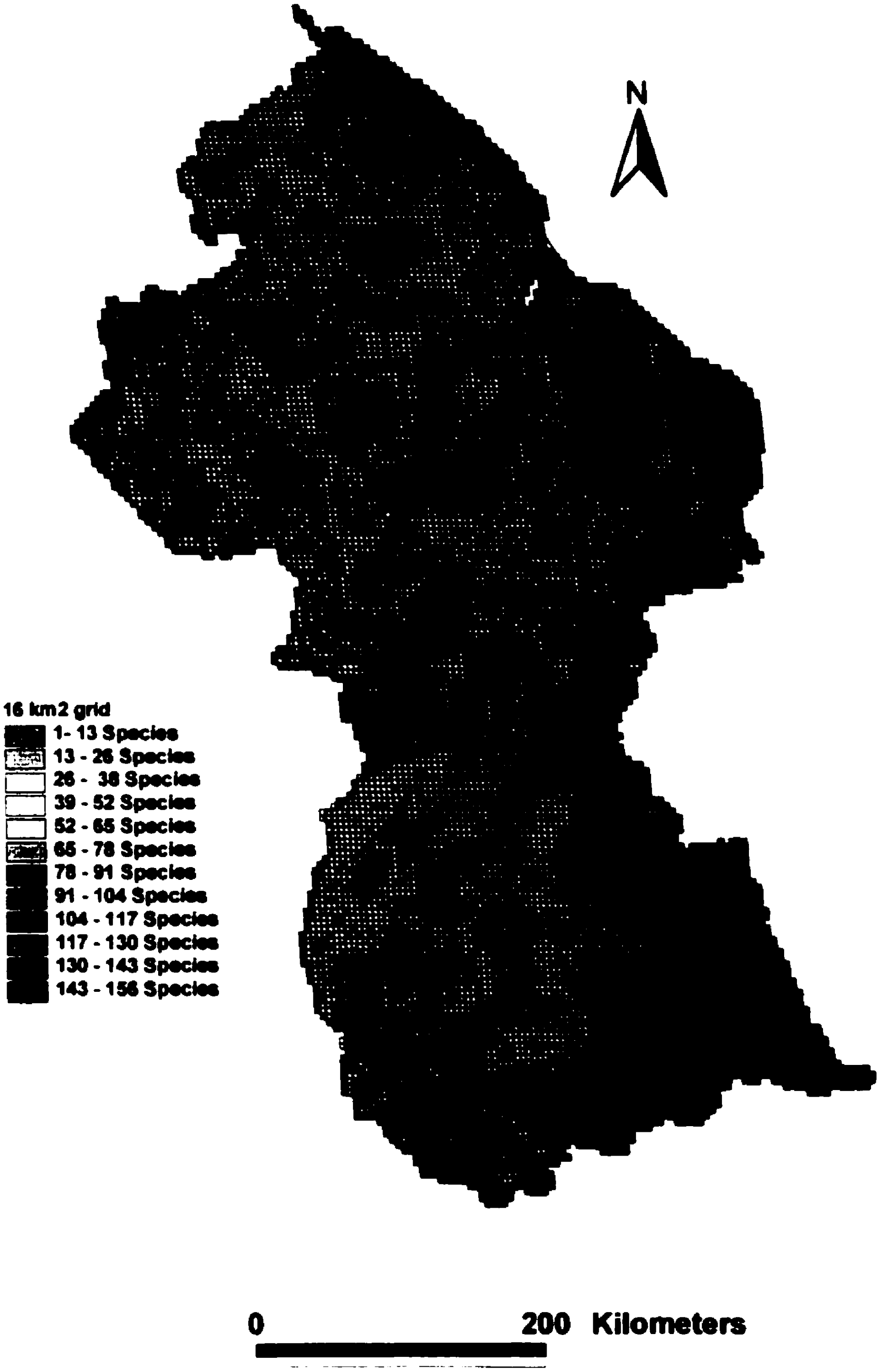


Figure 36b: Species Richness at a Grid Size of 64 km^2

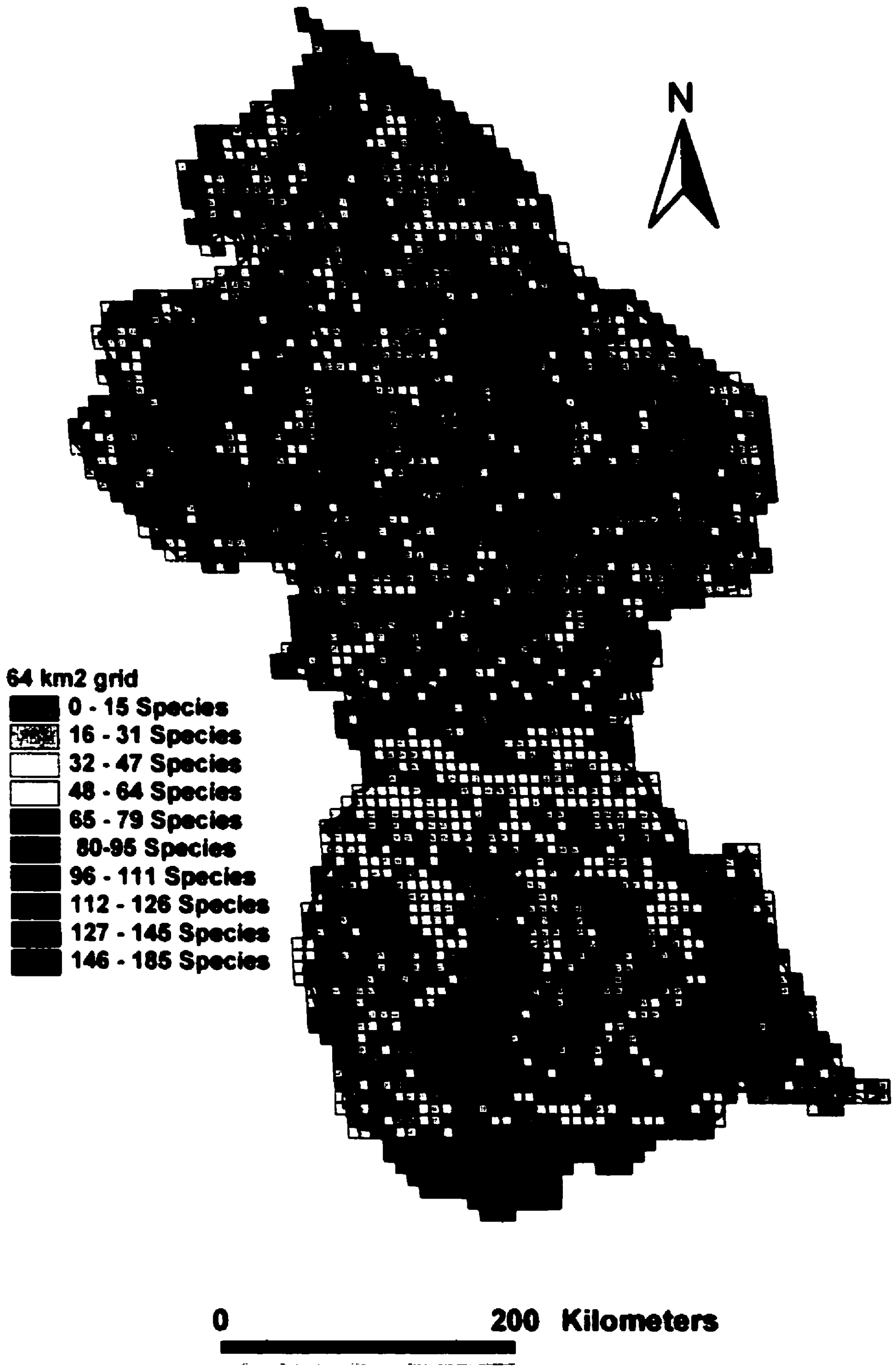


Figure 36c: Species Richness at a Grid Size of 256 km^2

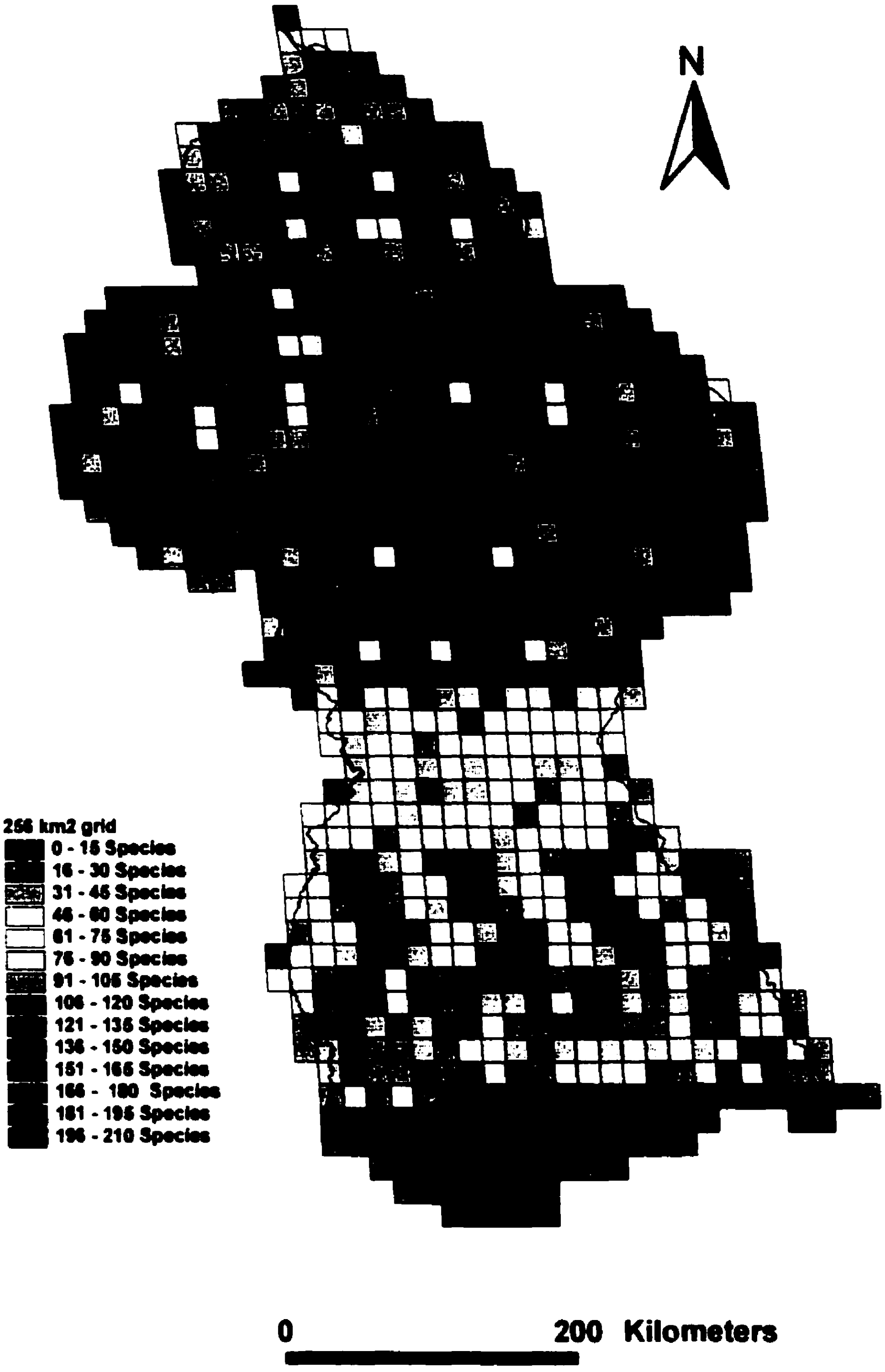


Figure 36d: Species Richness at a Grid Size of 1,024 km^2

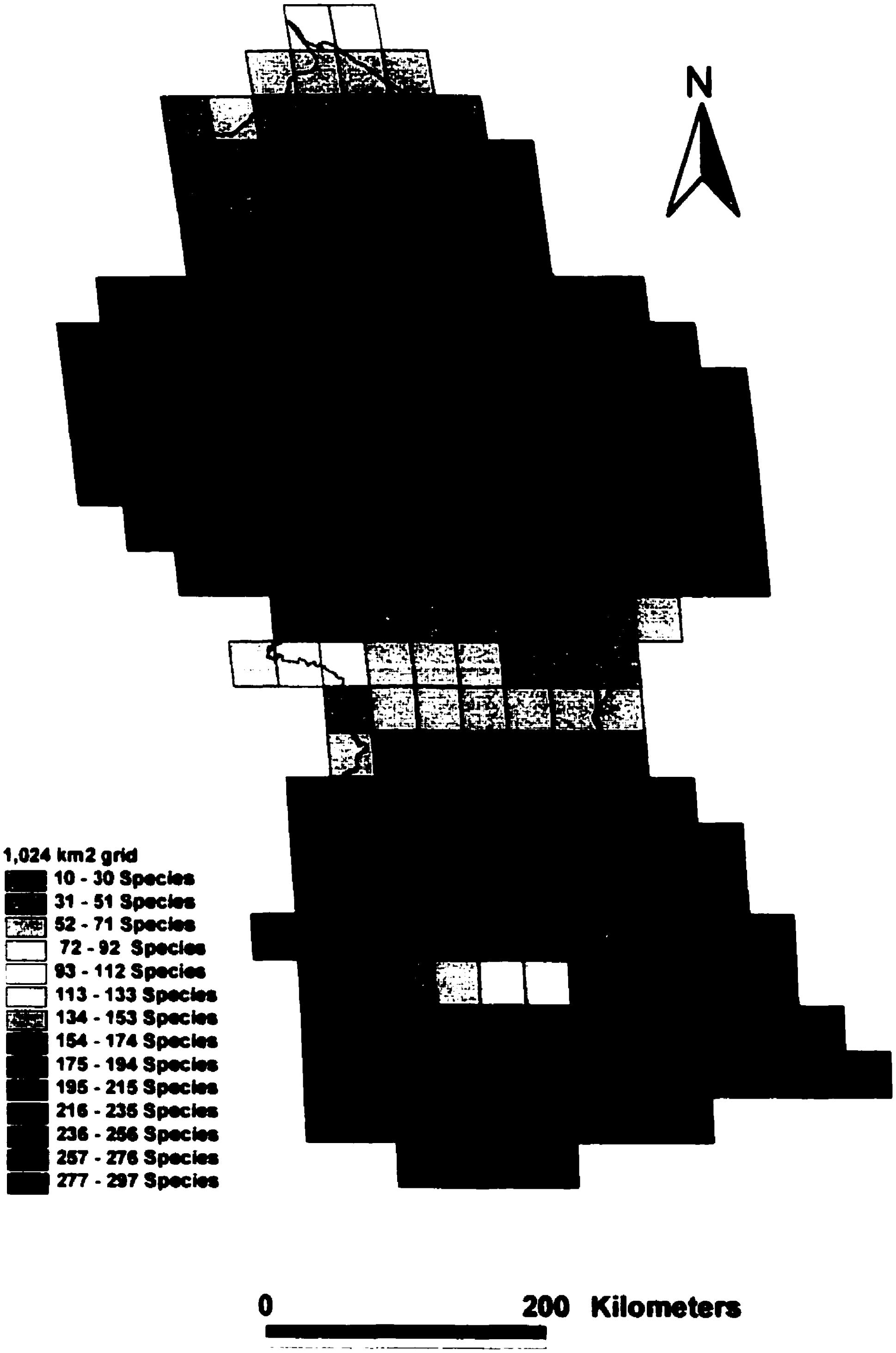


Figure 36e: Species Richness at a Grid Size of 4,096 km^2

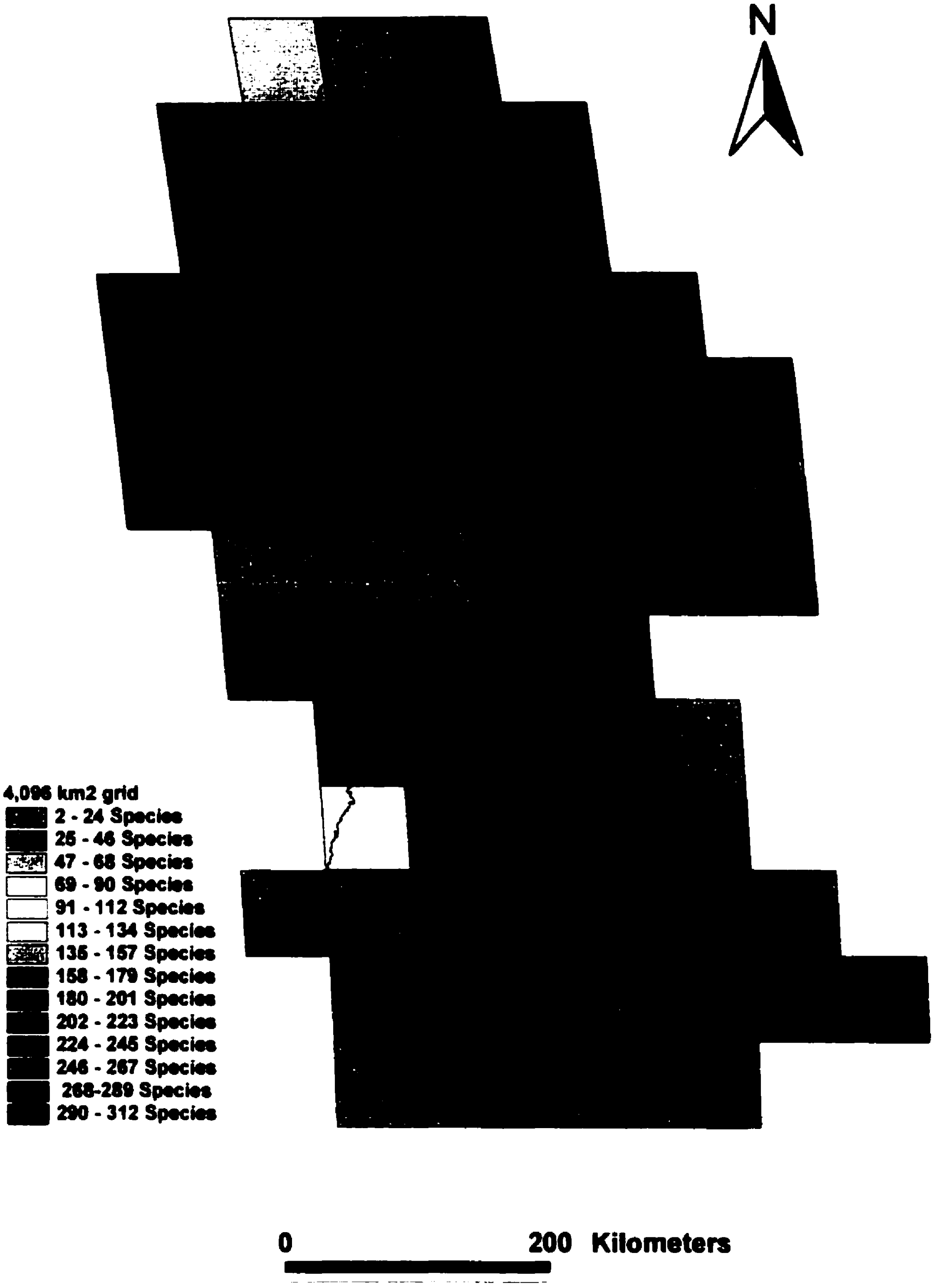


Figure 36f: Species Richness at a Grid Size of 16,384 km^2

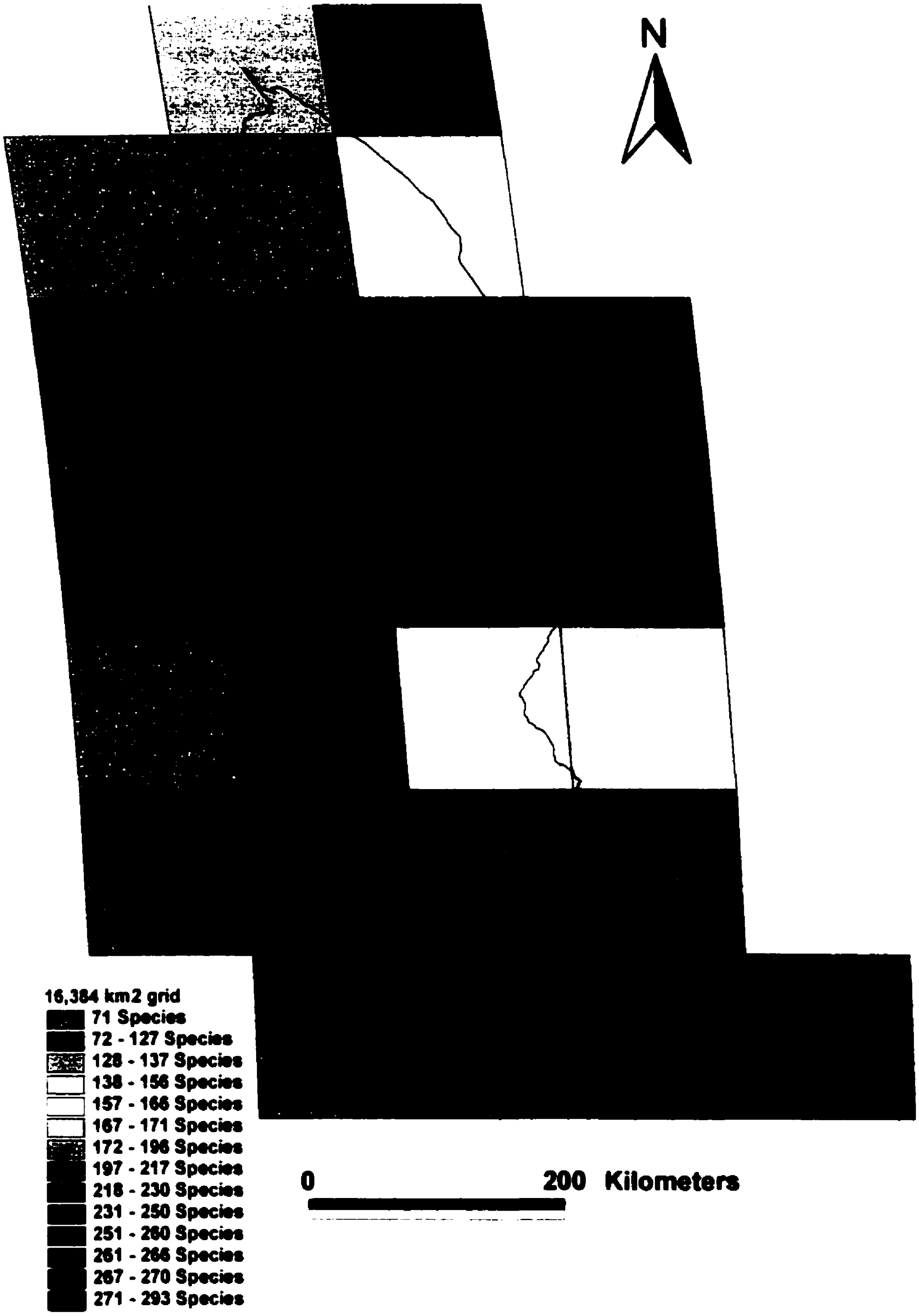


Figure 37: Coefficient of Variation of Richness for Different Grid Sizes

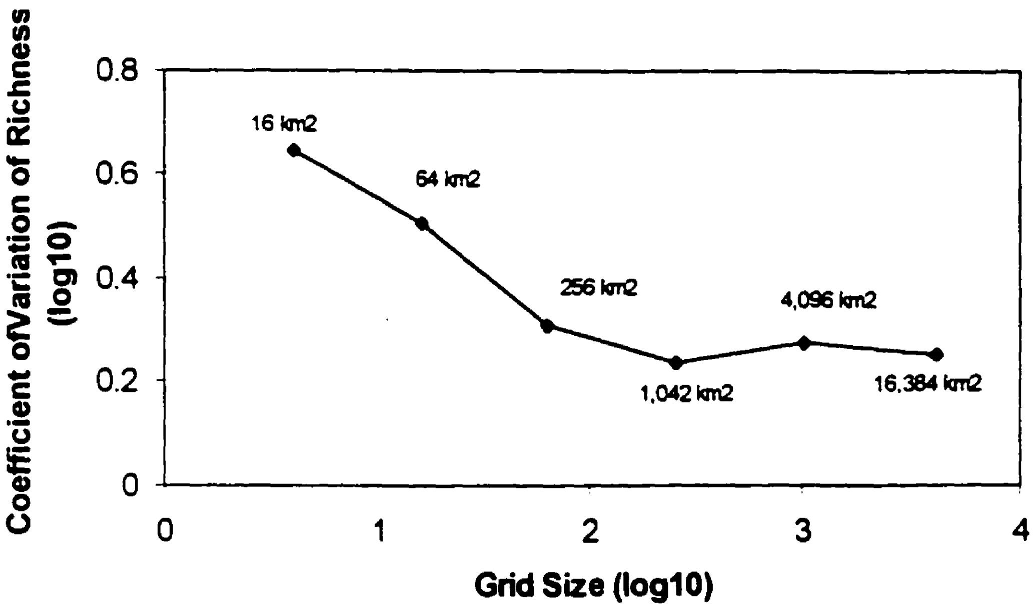


Figure 38a: Selected Priority Sites at 16 km^2

Figure 38b: Selected Priority Sites at 64 km^2

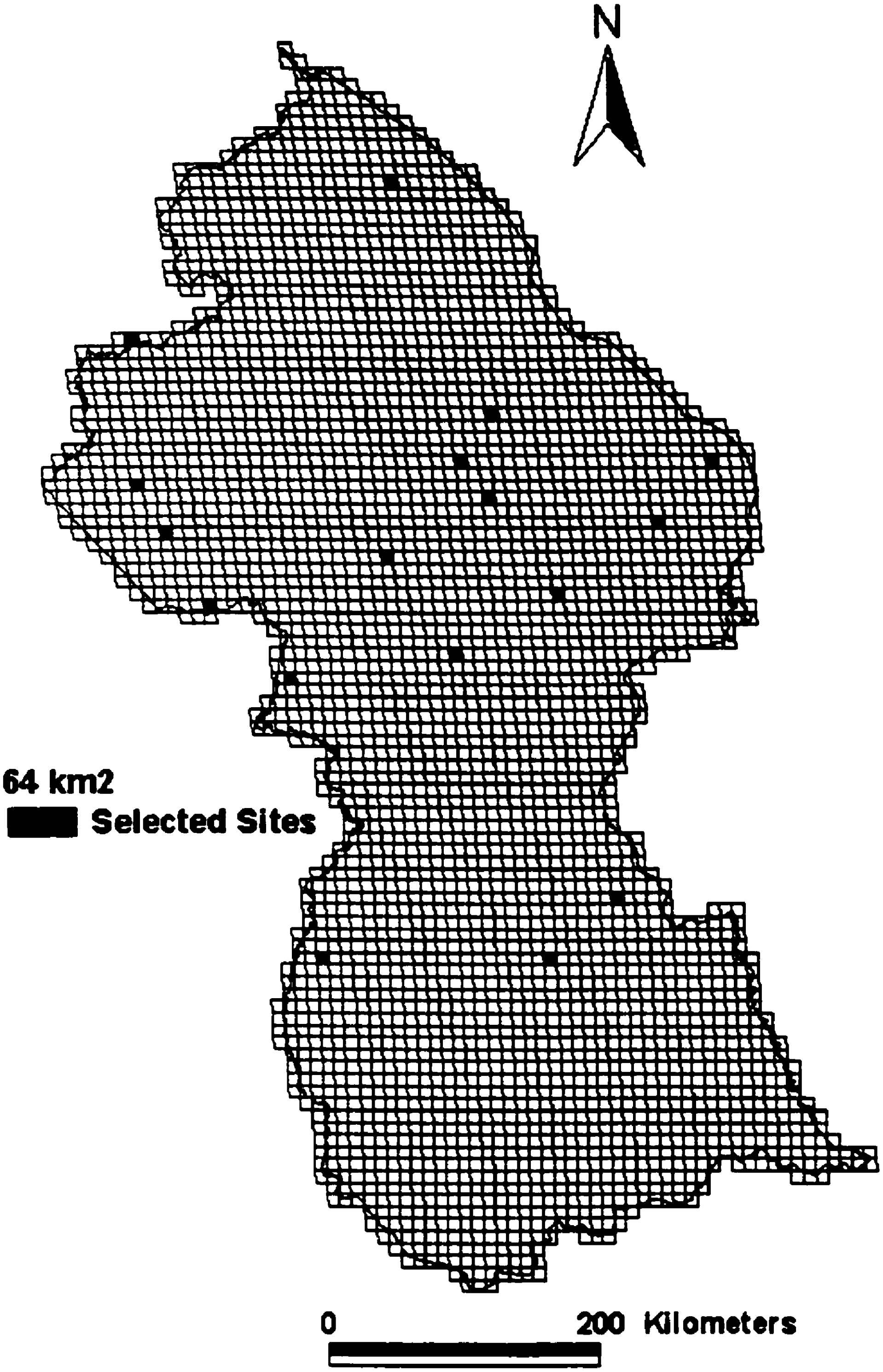


Figure 38c: Selected Priority Sites at 256 km^2

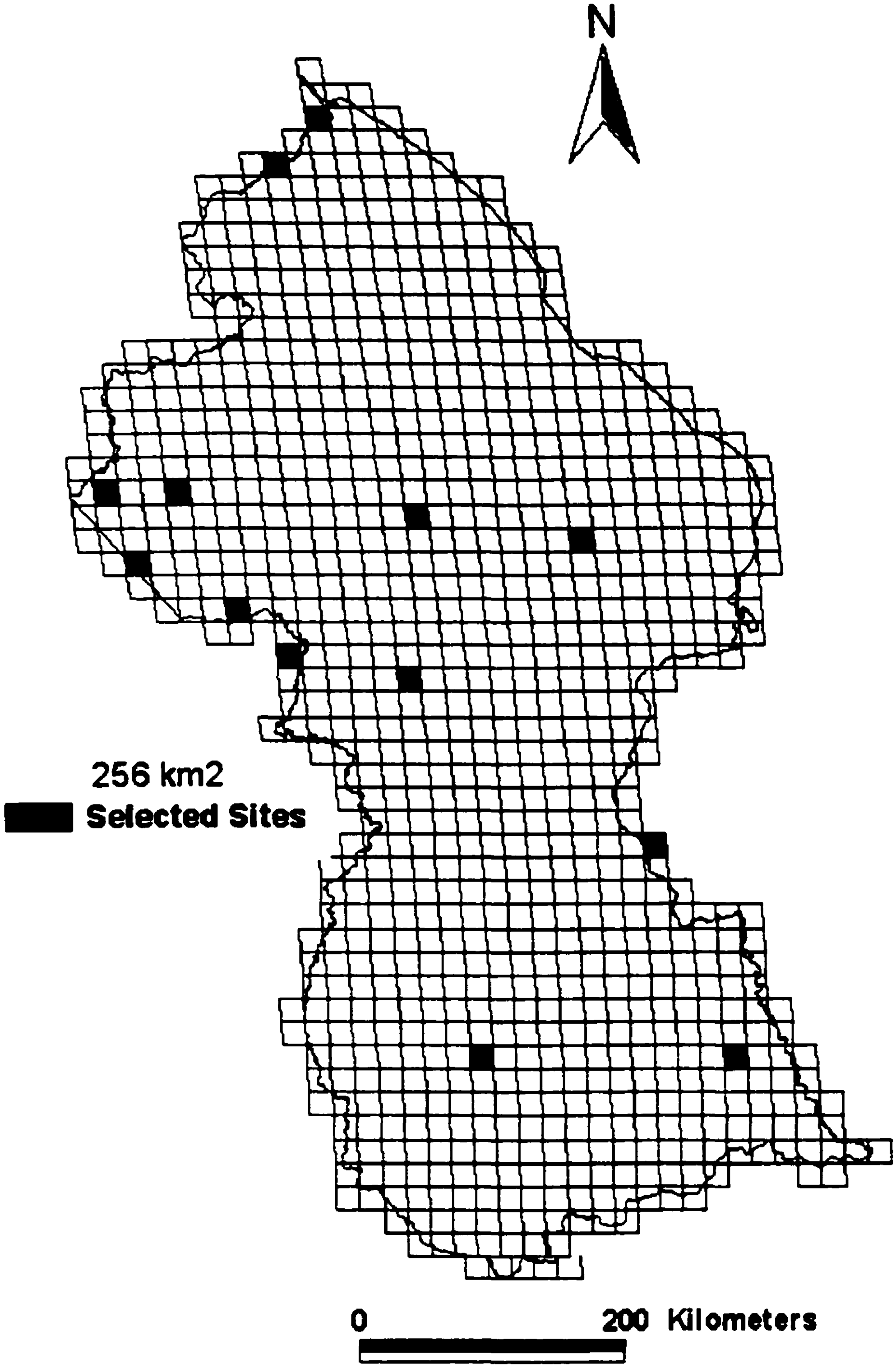


Figure 38d: Selected Priority Sites at 1,024 km^2

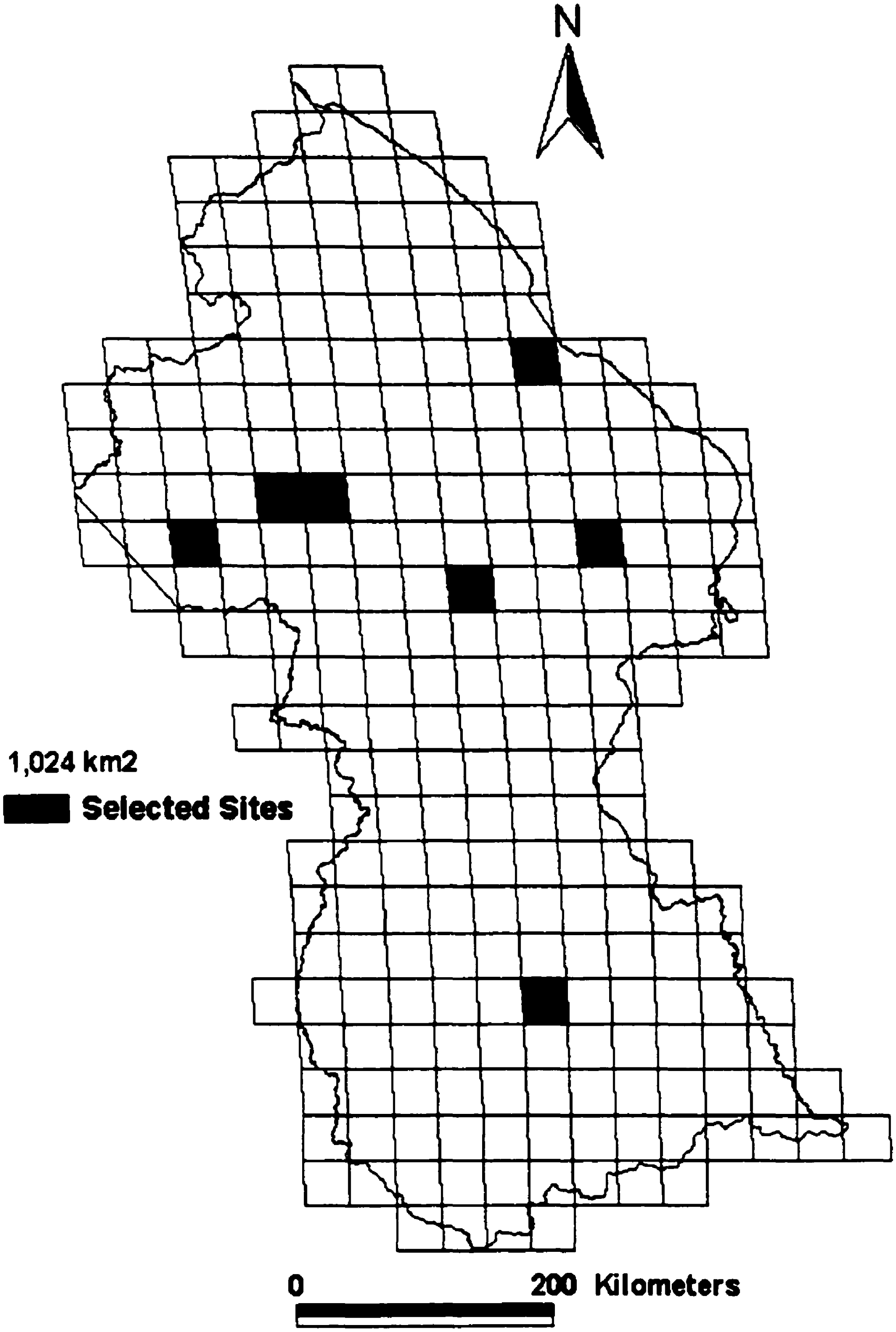


Figure 38e: Selected Priority Sites at 4,096 km^2

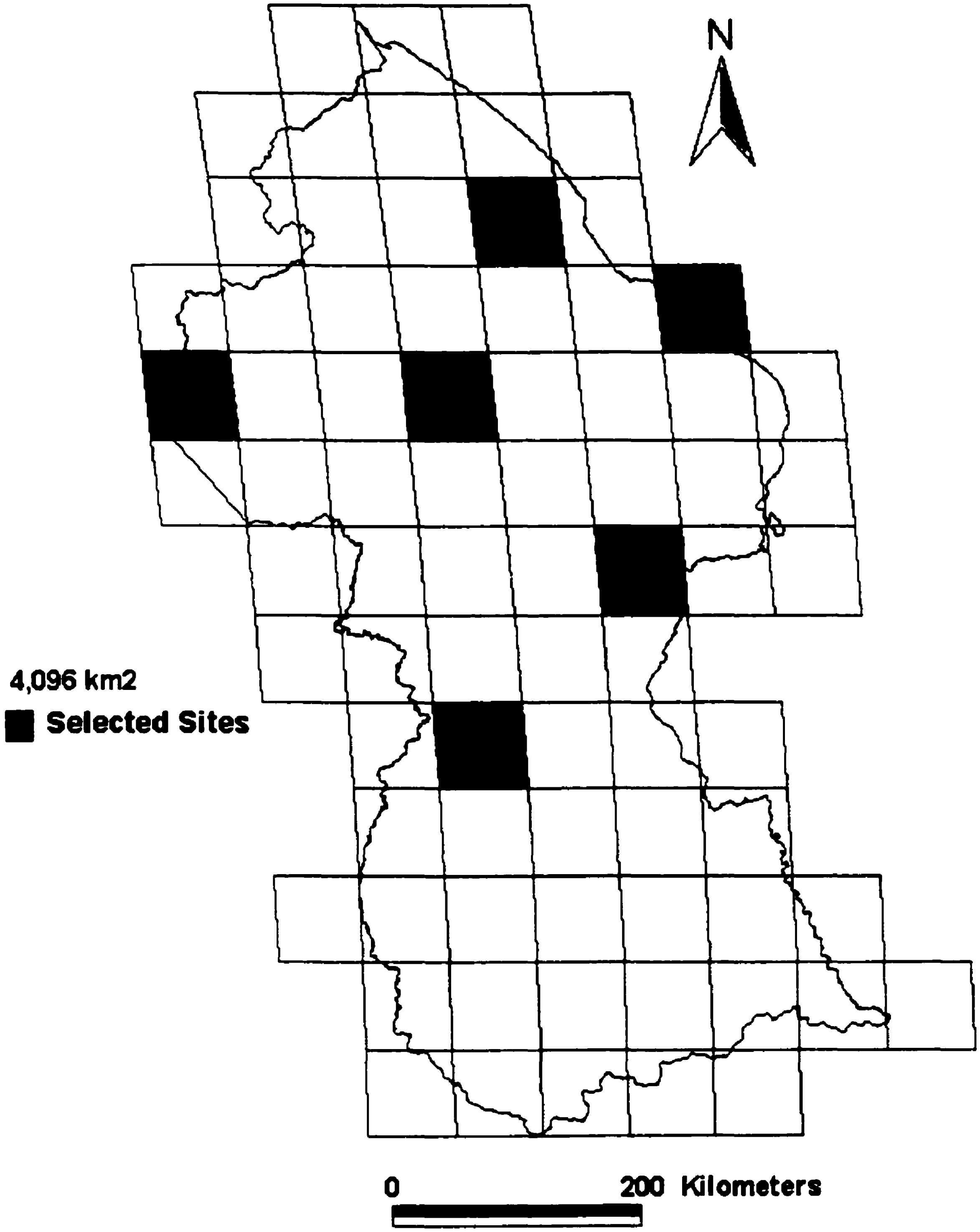
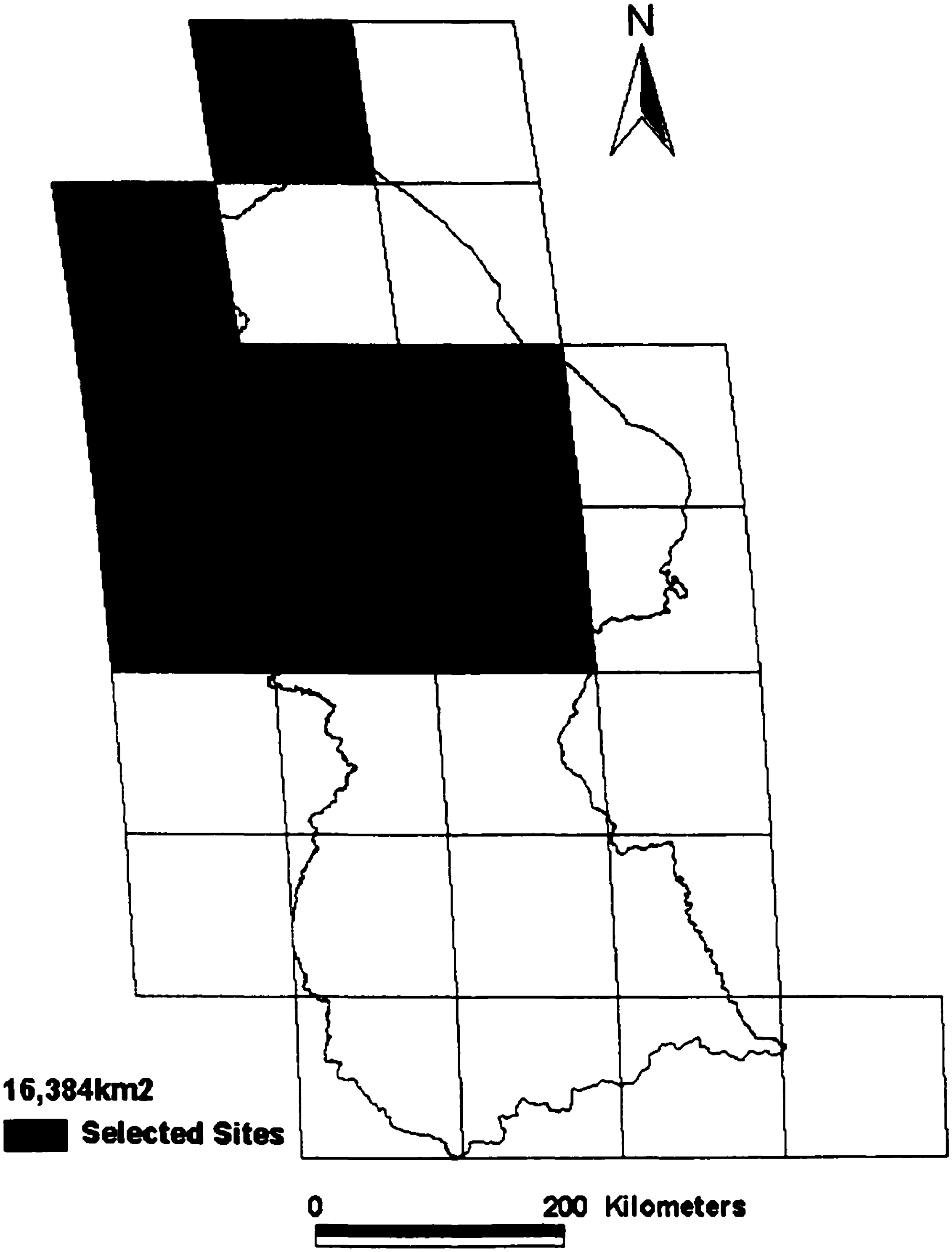


Figure 38f: Selected Priority Sites at 16,384 km^2



6.3.3 Cross-Taxon Congruency

The most interesting result is how the efficiency of cross taxon surrogacy changes with the size of the selection unit. At a selection unit size of 16 km^2, only four of the ten chosen taxonomic groups were effective surrogates (See Chapter 5 for details). At a selection unit size of 64 km^2, all groups were more effective surrogates for the target taxon group than random (Figures 39 a-t). For birds, amphibians were the only effective surrogates and all other groups performed better than random (Figures 39 a-b). As for understorey trees, it performed slightly better than the rest of the groups and all groups performed better than random (Figure 39 c-d). For ferns, understorey trees performed slightly better as a surrogate than the rest of the groups, however the rest of the groups were still effective surrogates and all performed better than random (Figure 39 e-f). For amphibians, sedges performed slightly better than the rest of the groups as a surrogate, however all groups were effective surrogates and performed better than random (Figure 39 g-h). For emergent trees, emergent trees were slightly better than the rest of the groups and amphibians and birds were slightly worse than the rest of the groups, however all groups performed better than random (Figure 39 i-j). For legumes, sedges were slightly better as a surrogate for legumes, however no groups were as effective as legumes, but the all performed better than random (Figure 39 k-l). For mammals, no groups were effective surrogates, and orchids performed worse than the rest of the groups. All performed better than random (Figure 39 m-n). For melastomes, only ferns were effective as a surrogate and understorey trees performed slightly better than the rest of the groups. All performed better than random (Figure 39 o-p). For orchids, orchids themselves performed slightly better than the rest of the groups and all performed better than random (Figures 39 q-r). Finally, for sedges, sedges performed only slightly better than the rest of the groups and they all performed better than random (Figures 39 s-t).

At the 256 km^2 –grid cell size, most groups were as effective as the target-group in capturing the nominated species in the dataset, with the exception of mammals and sedges (Figures 40 a-t). At the selection unit levels of 1,024 km^2, 4,096 km^2 and 16,384 km^2, so few sites were required to represent each species 3 times, that all groups approached equality in their effectiveness as a surrogate, although they all performed better than random.

Figure 39: (a) Comparison of Areas when Birds are the Target Group at 64 km^2; (b) Species Accumulation Curves when Birds are the Target Group at 64 km^2

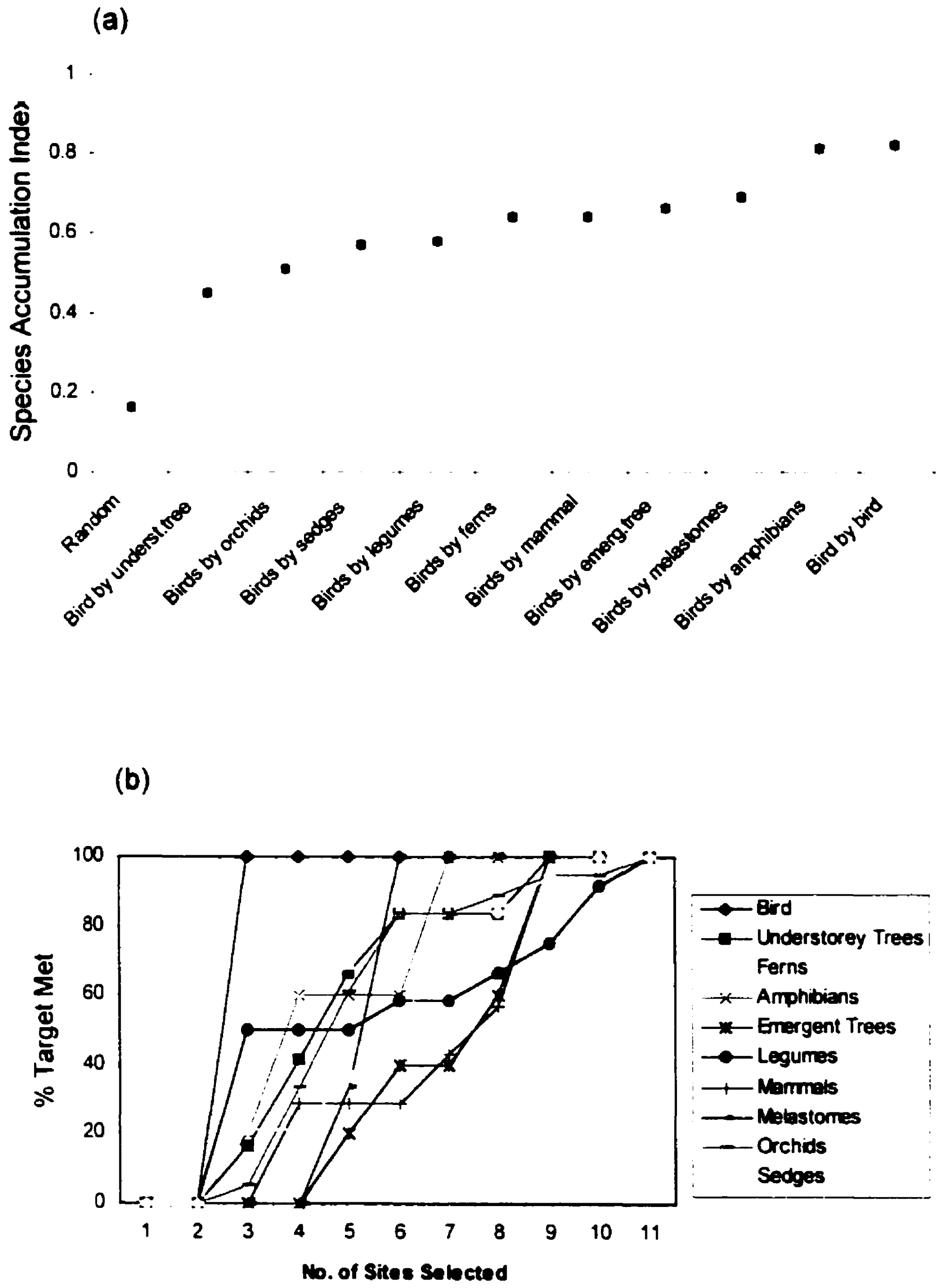


Figure 39: (c) Comparison of Areas when Understorey Trees are the Target Group at 64 km^2; (d) Species Accumulation Curves when Understorey Trees are the Target Group at 64 km^2

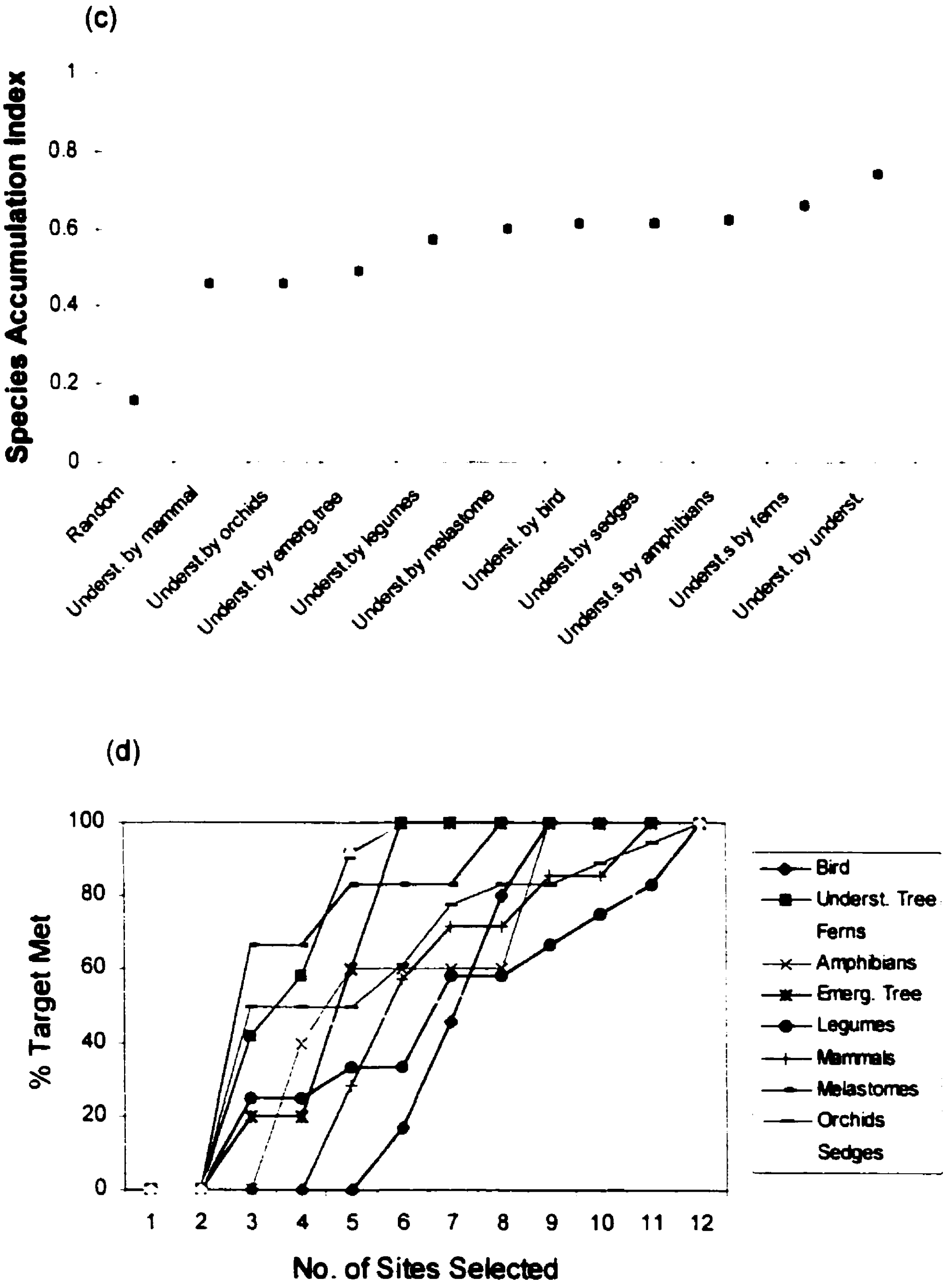


Figure 39: (e) Comparison of Areas when Ferns are the Target Group at 64 km^2; (f) Species Accumulation Curves when Ferns are the Target Group at 64 km^2

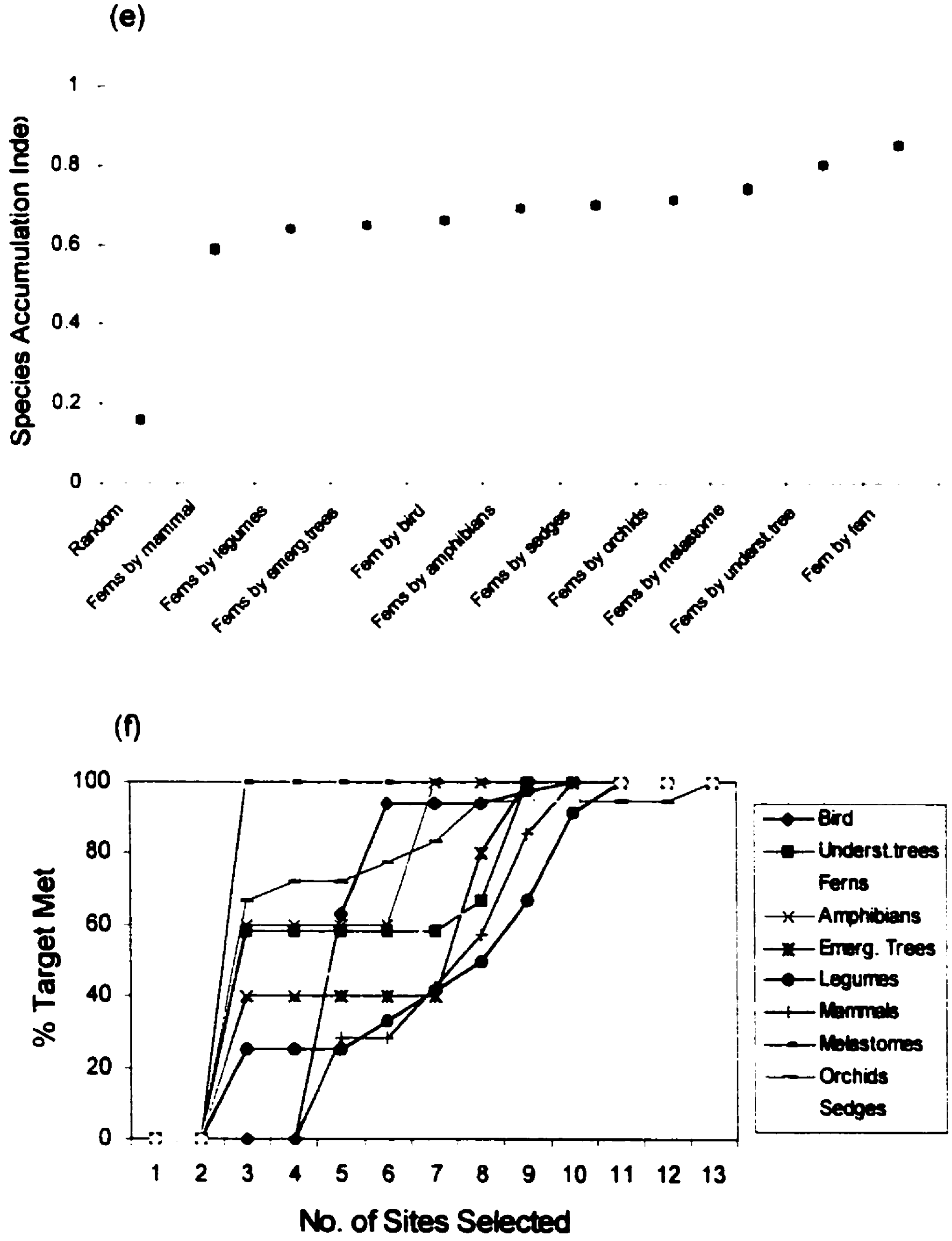
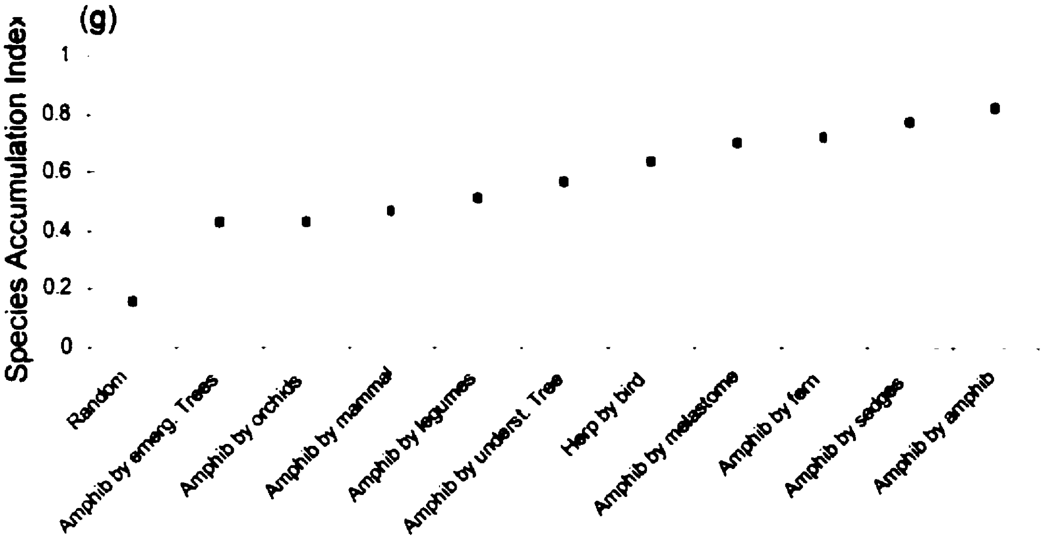


Figure 39: (g) Comparison of Areas when Amphibians are the Target Group at 64 km^2; (h) Species Accumulation Curves when Amphibians Trees are the Target Group at 64 km^2



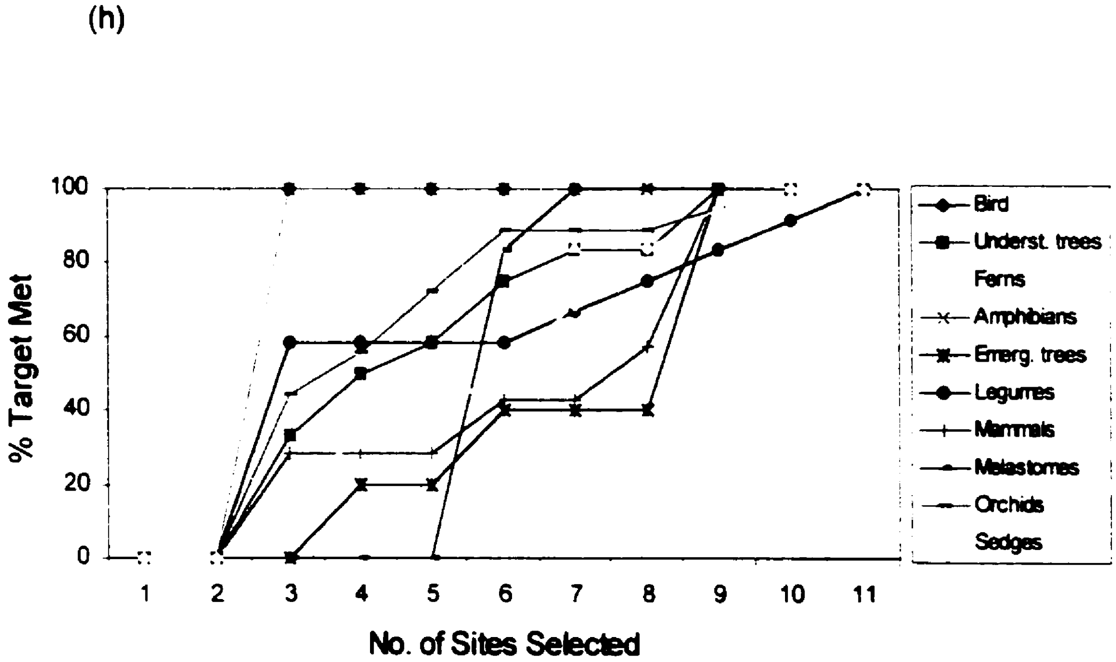


Figure 39: (i) Comparison of Areas when Emergent Trees are the Target Group at 64 km^2; (j) Species Accumulation Curves when Emergent Trees are the Target Group at 64 km^2

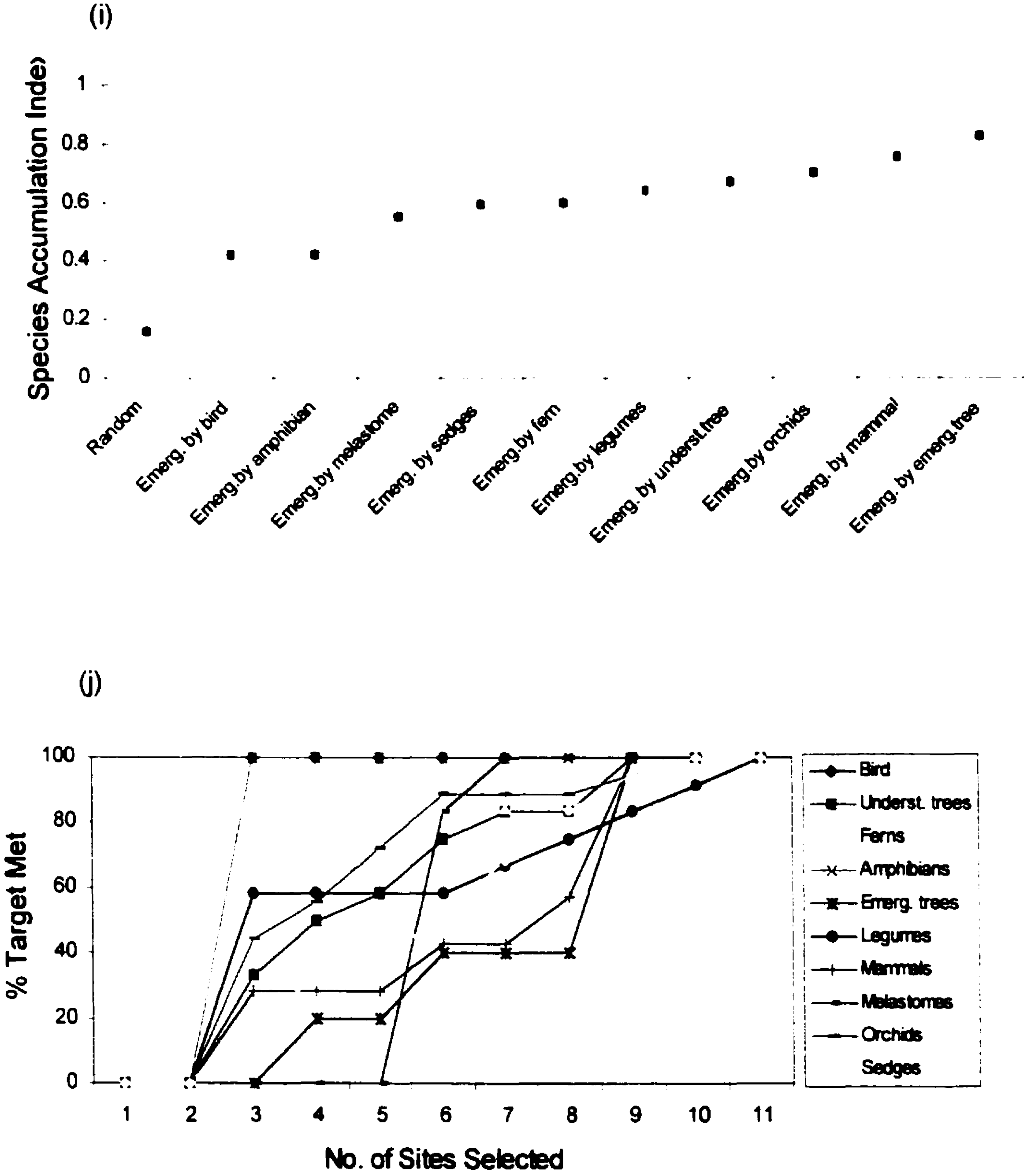


Figure 39: (k) Comparison of Areas when Legumes are the Target Group at 64 km^2; (l) Species Accumulation Curves when Legumes are the Target Group at 64 km^2

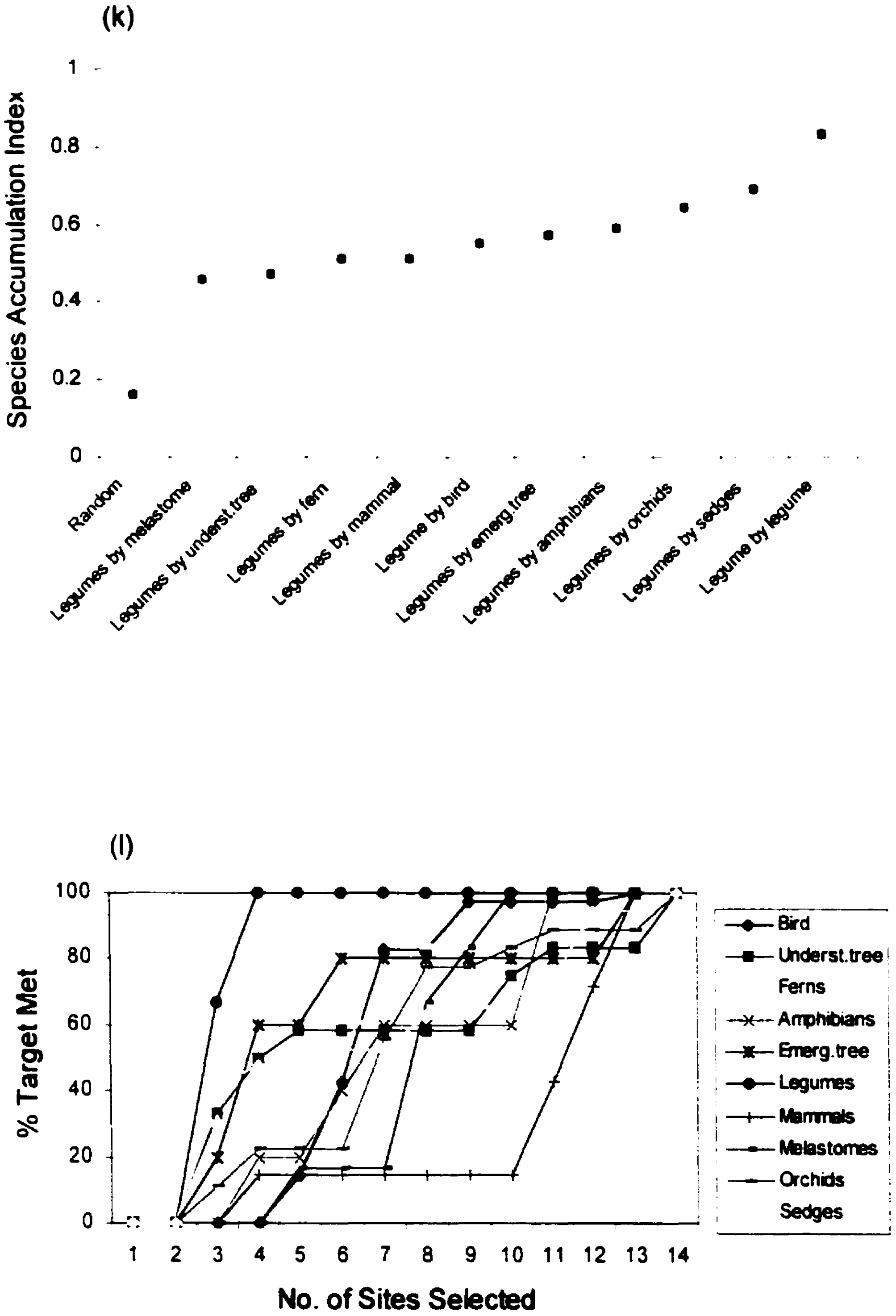


Figure 39: (m) Comparison of Areas when Mammals are the Target Group at 64 km^2; (n) Species Accumulation Curves when Mammals are the Target Group at 64 km^2

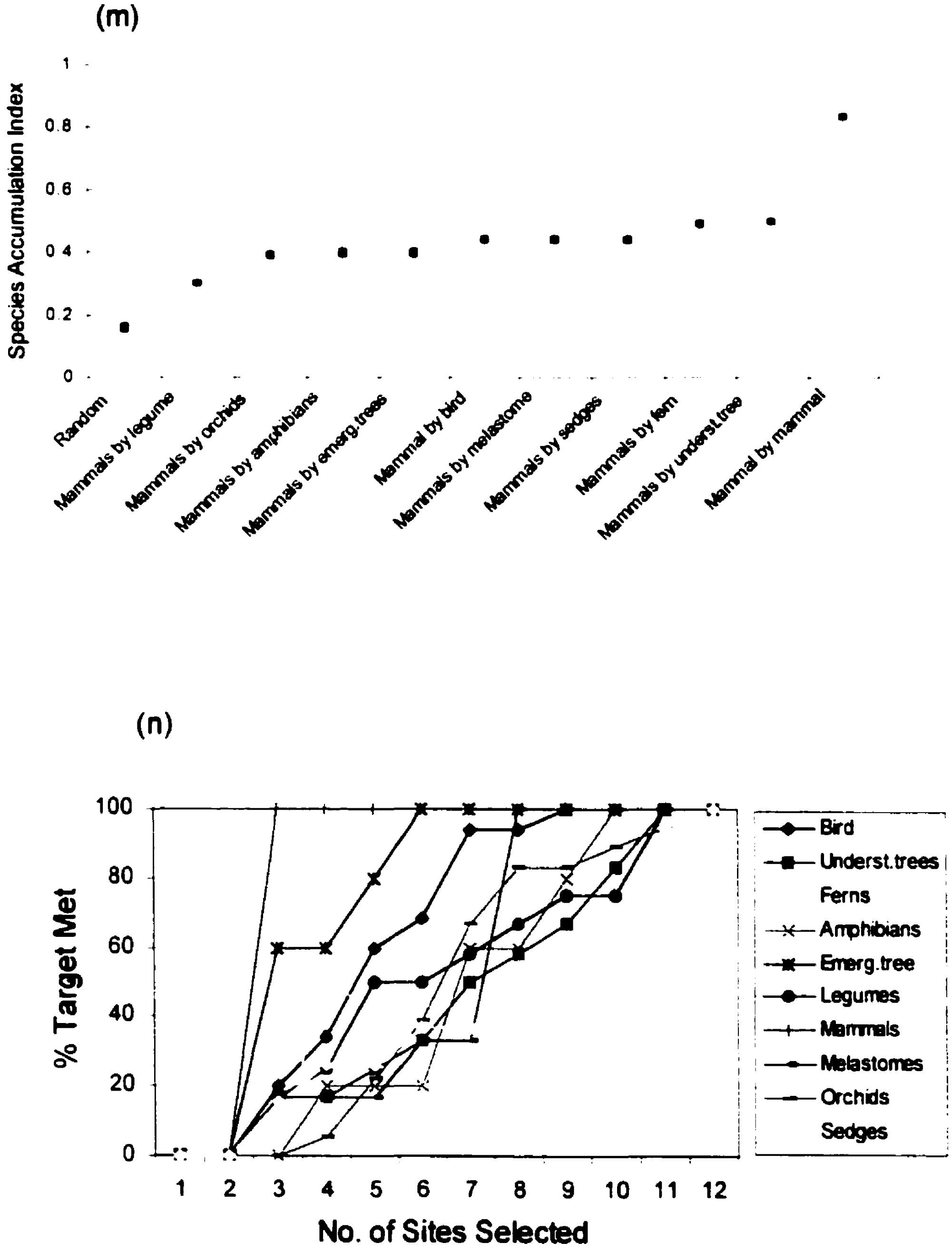


Figure 39: (o) Comparison of Areas when Melastomes are the Target Group at 64 km^2; (p) Species Accumulation Curves when Melastomes are the Target Group at 64 km^2

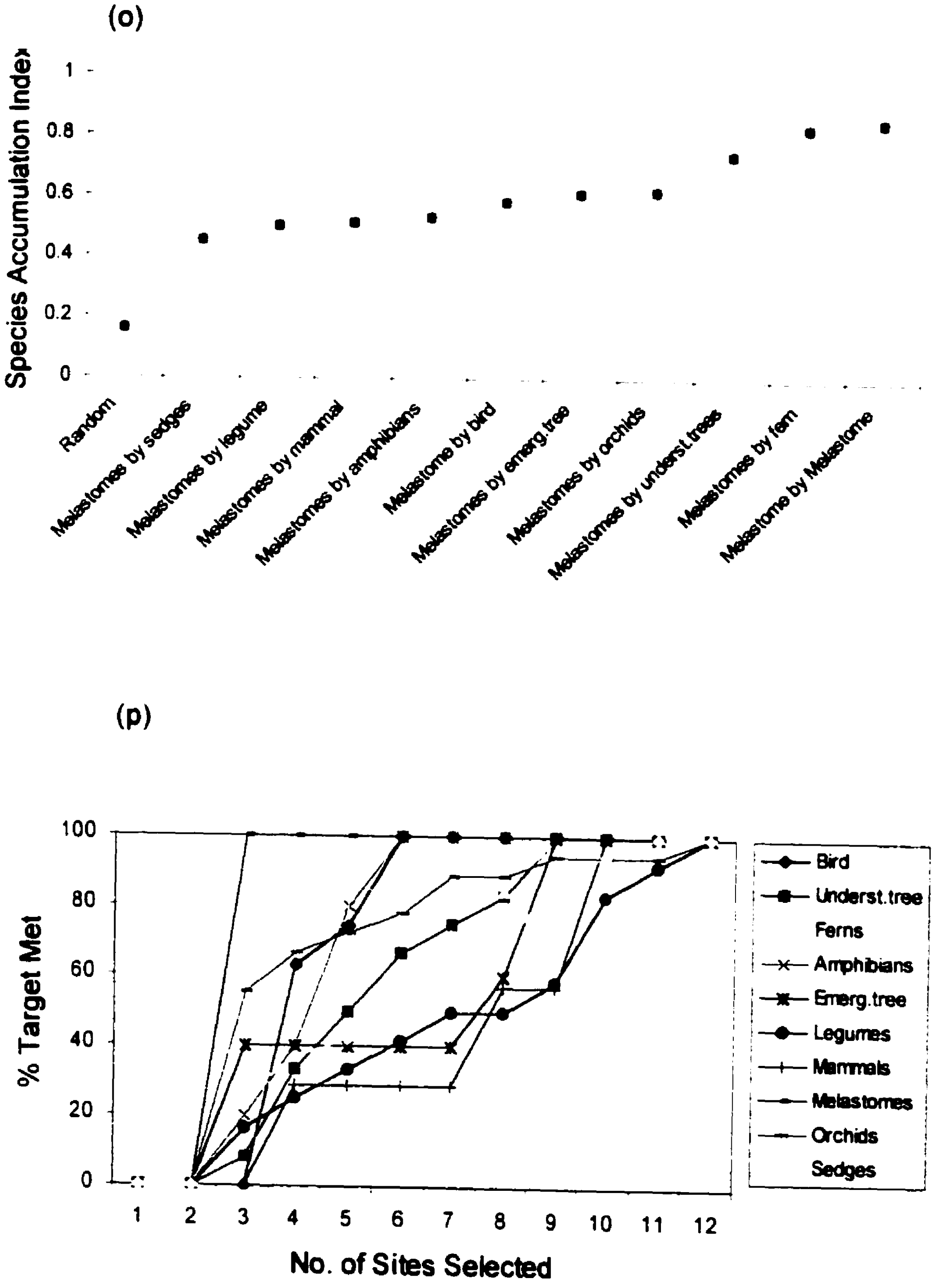


Figure 39: (q) Comparison of Areas when Orchids are the Target Group at 64 km^2; (r) Species Accumulation Curves when Orchids are the Target Group at 64 km^2

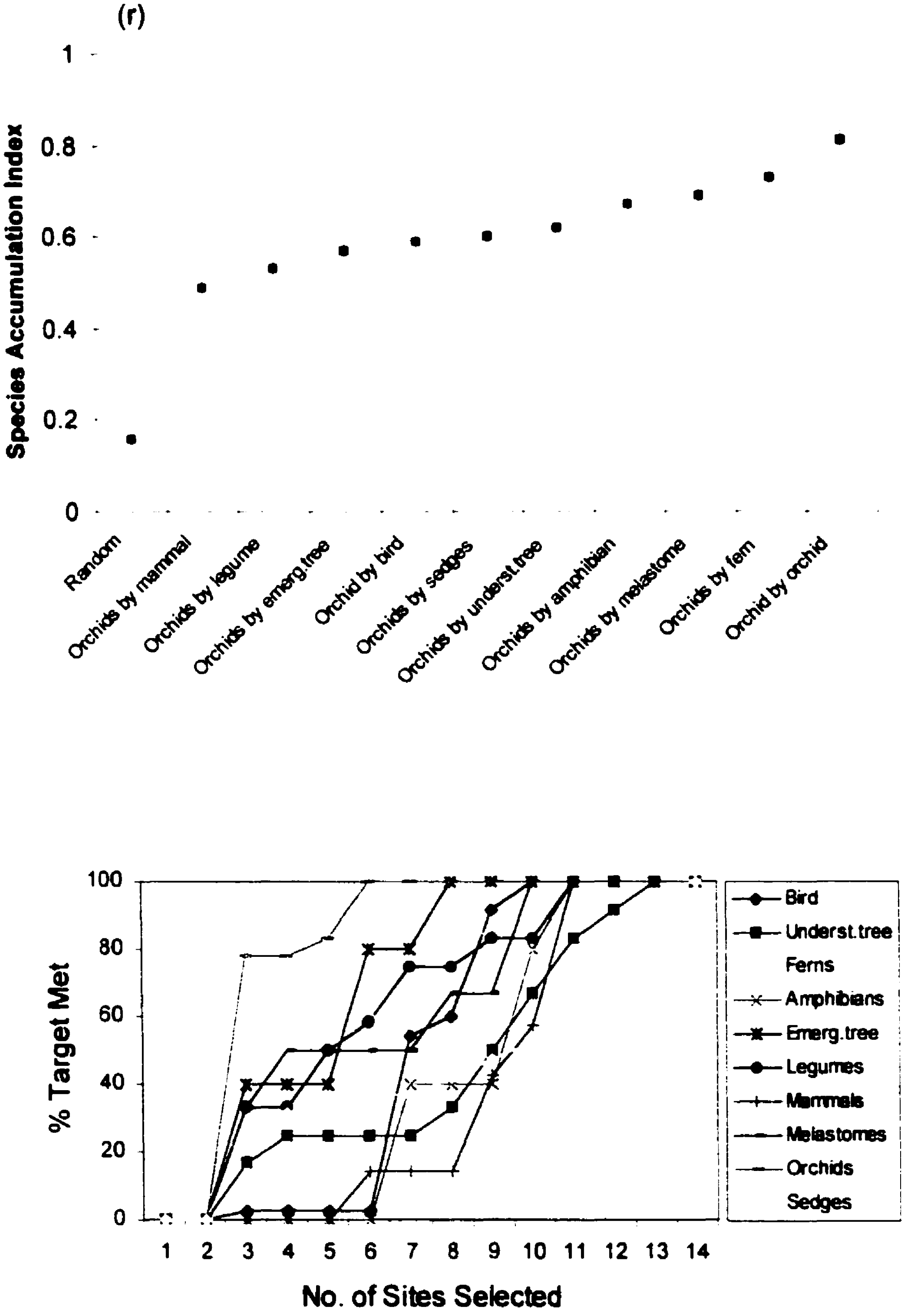
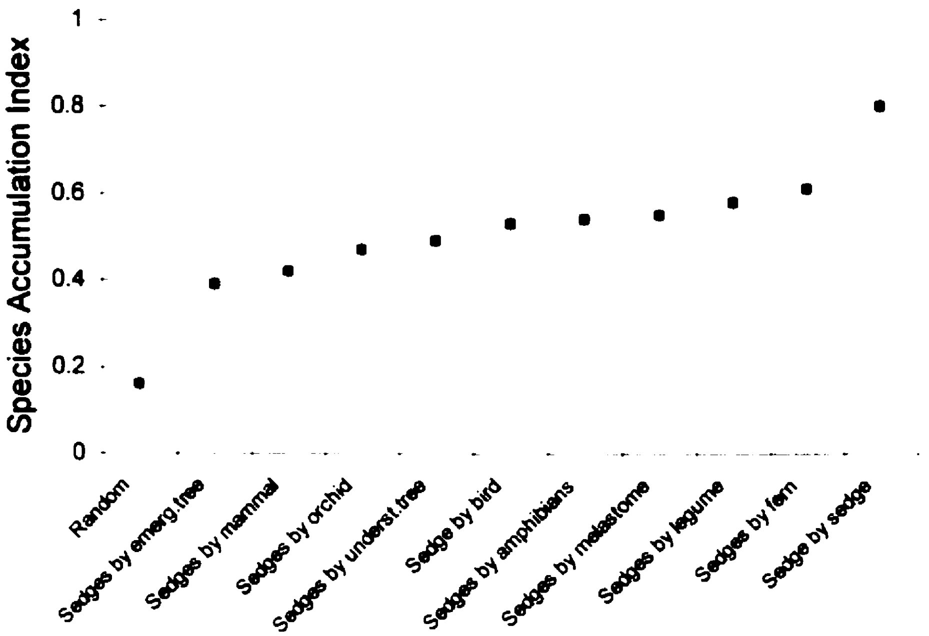


Figure 39: (s) Comparison of Areas when Sedges are the Target Group at 64 km^2; (t) Species Accumulation Curves when Sedges are the Target Group at 64 km^2

(s)



(t)

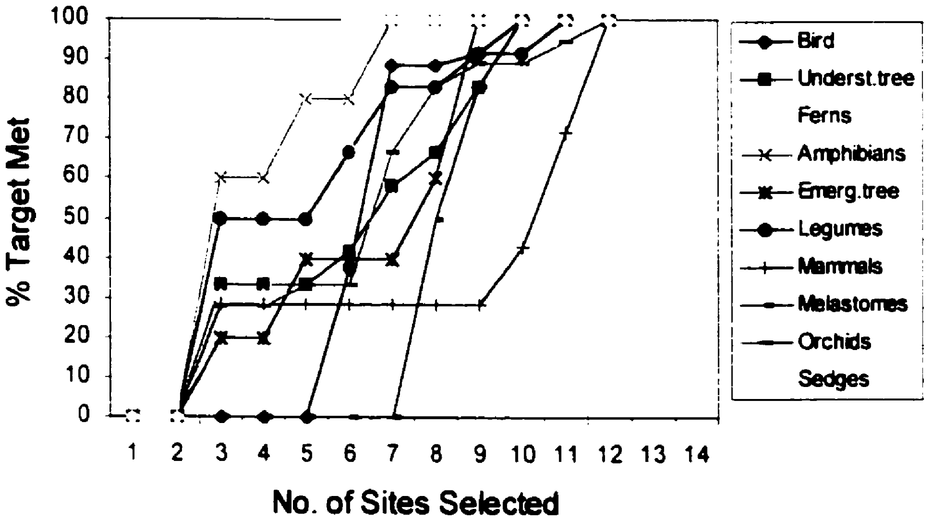


Figure 40: (a) Comparison of Areas when Birds are the Target Group at 256 km^2; (b) Comparison of Areas when Understorey Trees are the Target Group at 256 km^2

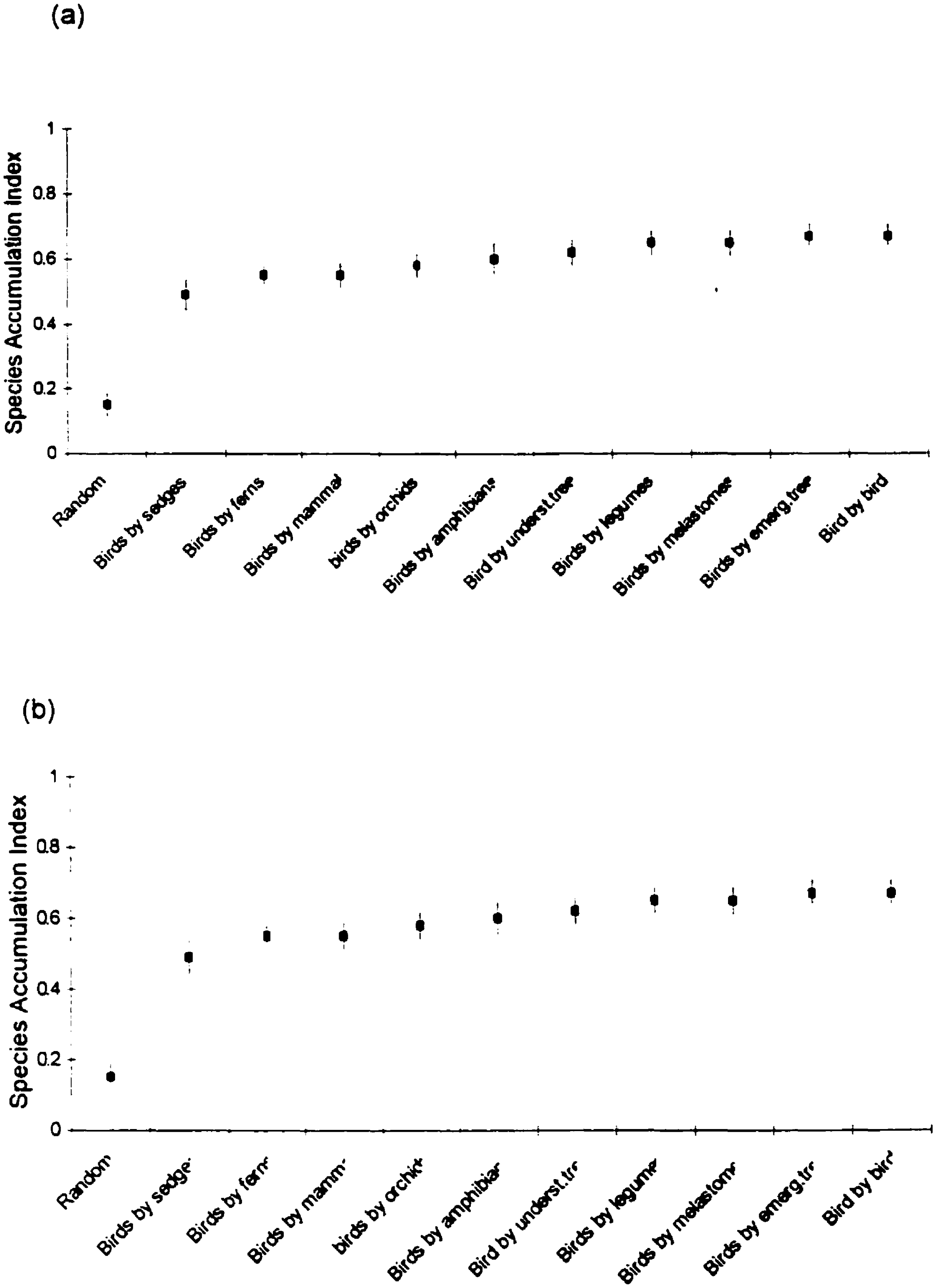


Figure 40: (c) Comparison of Areas when Ferns are the Target Group at 256km^2; (d) Comparison of Areas when Amphibians are the Target Group at 256km^2;

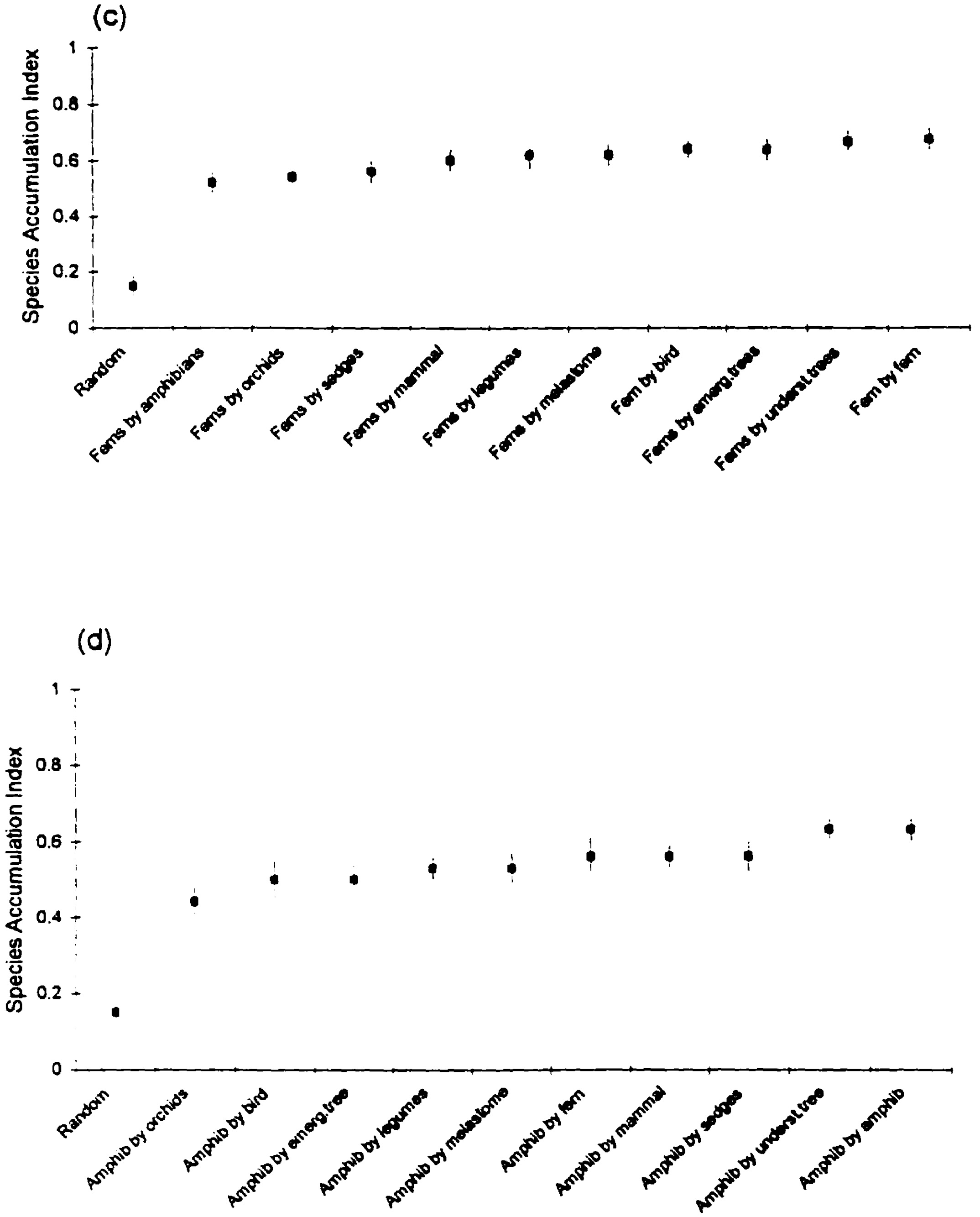


Figure 40: (e) Comparison of Areas when Emergent Trees are the Target Group at 256 km^2; (f) Comparison of Areas when Legumes are the Target Group at 256 km^2

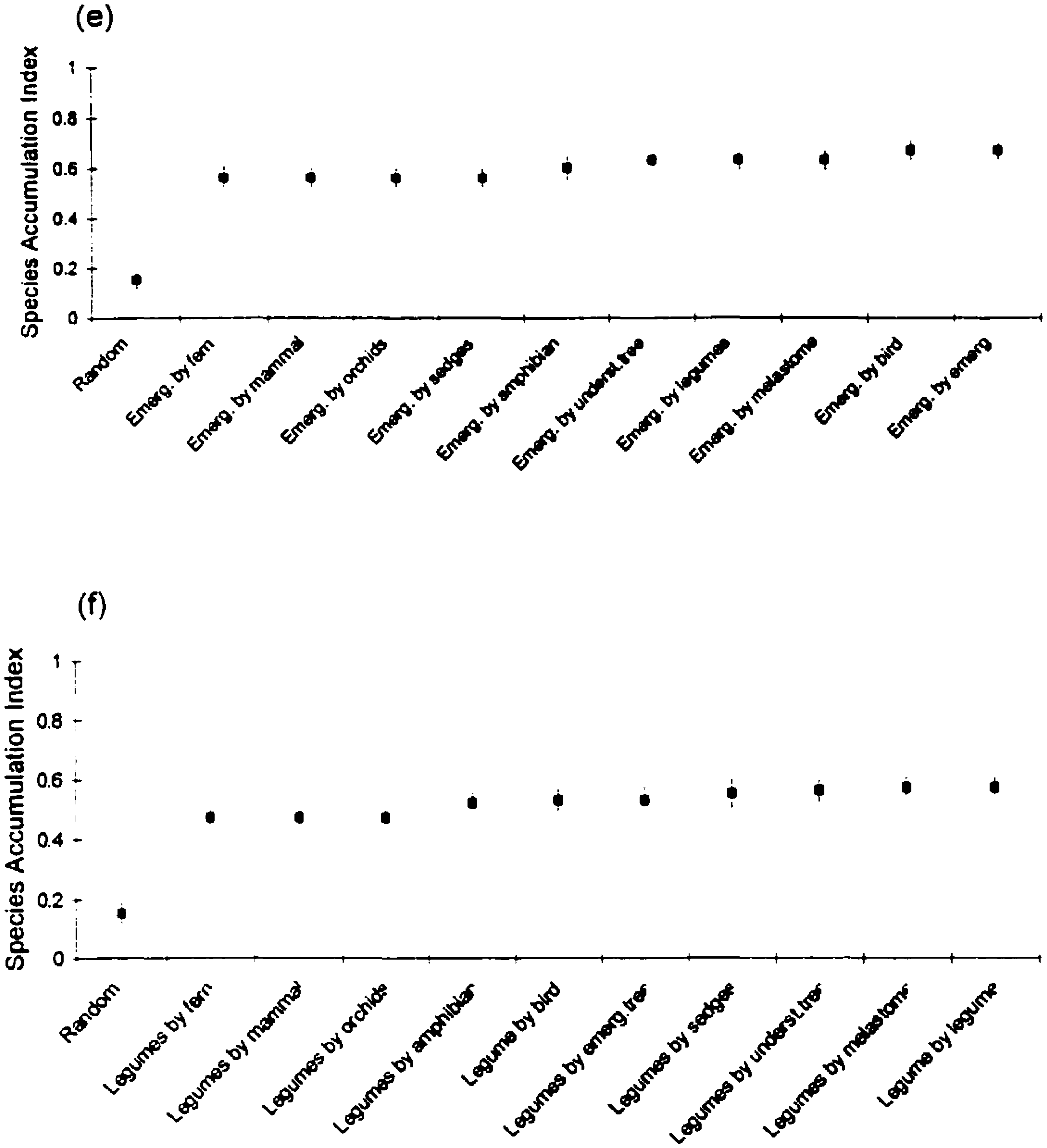


Figure 40: (g) Comparison of Areas when Mammals are the Target Group at 256 km^2; (h) Comparison of Areas when Melastomes are the Target Group at 256 km^2;

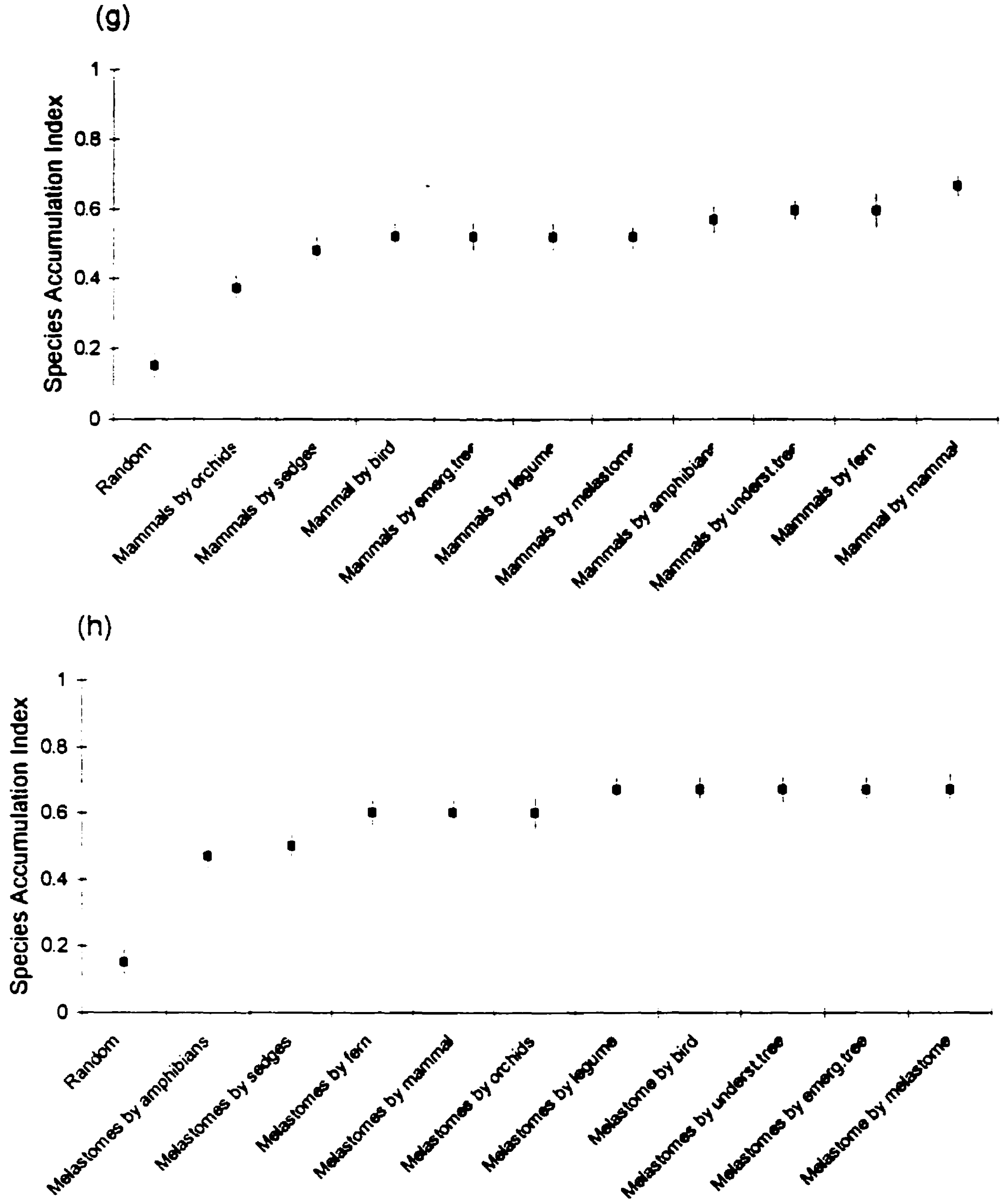
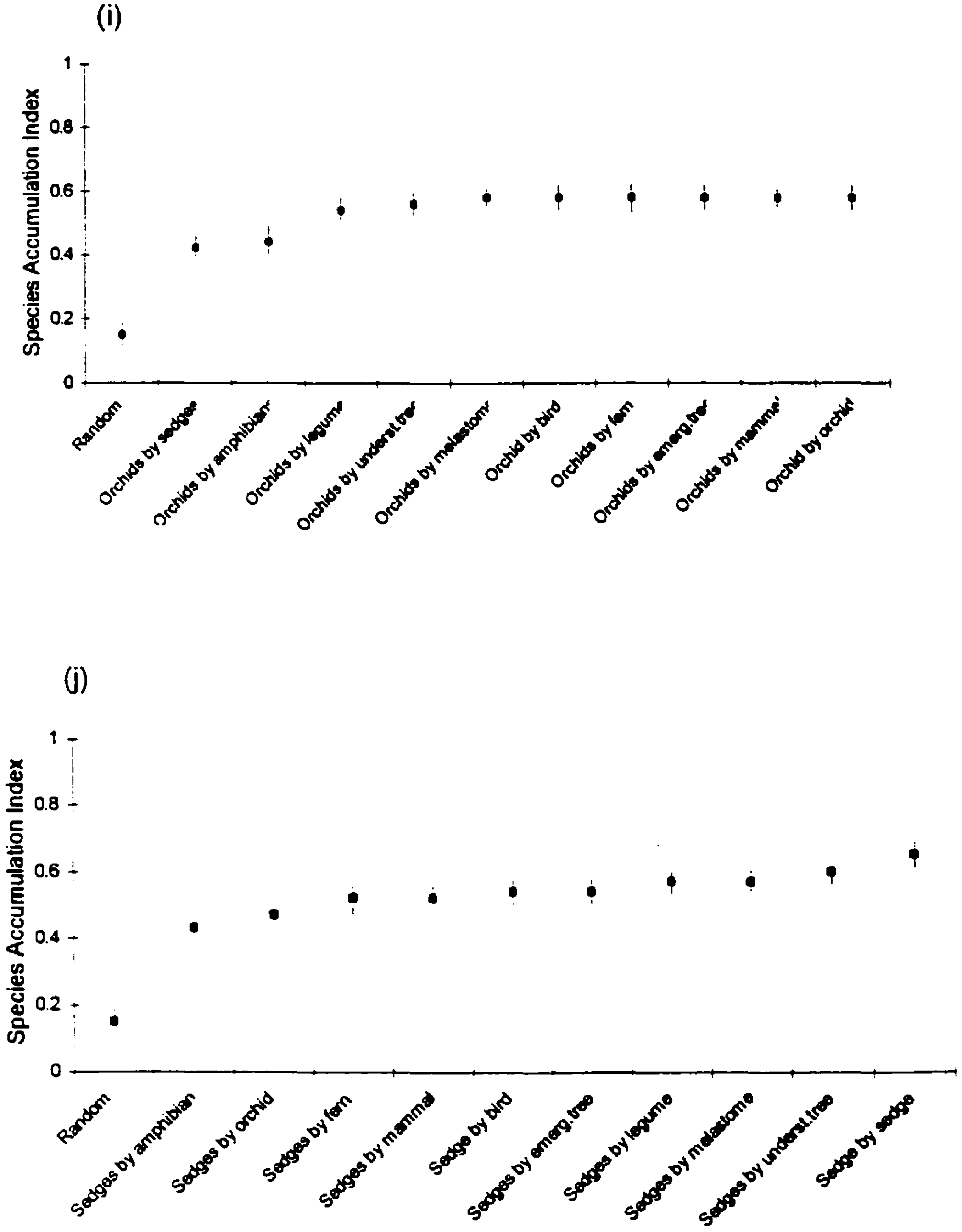


Figure 40: (i) Comparison of Areas when Orchids are the Target Group at 256 km²; (j) Comparison of Areas when Sedges are the Target Group at 256 km²



6.4 DISCUSION

Spatial scale appears to be a very important consideration in the representation of biodiversity as measured by species richness and the selection of priority biodiversity sites. Although this chapter only examined the influence of altering the size of selection units, the results clearly show that different sizes of selection units produce different results in terms of the recorded species richness of an area, the location of priority biodiversity sites, and the efficiency of different taxonomic groups to act as surrogates for one another. These results have significant implications for conservation decision-making. The results from the analyses of the coefficient of variation of richness and the minimum set selection demonstrate that if the results were to be used for decisions on the location and importance of biodiversity sites for a network of protected areas, different locations and emphasis would be allocated for protection depending upon the size of the selection unit used.

The debate surrounding whether different taxonomic groups can be used as surrogates to represent other groups (Prendergast *et al.* 1993, Lawton *et al.* 1994, Flather *et al.* 1997, Howard *et al.* 1998, Van Jaarseveld *et al.* 1998), must be re-examined in light of these results. At selection unit sizes below 256 km^2, the effectiveness of one taxonomic group to act as a surrogate for other groups is dependent upon the spatial distribution of the species within each taxonomic group and whether those species divide up the landscape in a similar manner to the target-group, and to some degree share the same ecological requirements. At larger selection unit sizes, the number of total grid cells is greatly reduced and each grid cell contains more species. At these sizes, most taxonomic groups appear to be very effective at representing the other groups. This finding is very important in the debate surrounding how to measure biodiversity, especially with regards to measurements involving species and the assumptions that indicator groups of species are representative of the overall biodiversity of an area. This chapter clearly shows that the efficiency of one taxon to act as an indicator for other taxa is depend on the scale at which the efficiency is measured.

6.4.1 Species Richness

Local species richness is a result of an interaction of history and current ecological processes (Lawton *et al.* 1994), although the relative contribution of these at a given spatial scale will vary among taxa, and for any given taxa, will vary with spatial scales. Significant determinants of species diversity are likely to include environmental and habitat heterogeneity, area, and the size of the regional species pool (a product of history) (Ricklefs 1987). Patterns of species turnover or beta diversity are more likely to be driven by biogeographic history, but are also dependent upon the scale of comparison. Many researchers have argued that there are strong ecological and evolutionary reasons for assessing biodiversity at the ecosystem or landscape level (gamma diversity level) (Noss and Harris 1986). These reasons include: a) incorporating the beta diversity of different taxonomic groups, b) considering the habitat requirement of species that are wide-ranging or sensitive to human disturbance; and c) integrating ecosystem processes at scales larger than a small patch (Davis and Stoms 1996). Another strong argument is that selection units smaller than those representing a landscape are not large enough to maintain biodiversity in the long term. The results from this study indicate that if landscape-level selection units were to be used to represent species richness and select priority biodiversity sites (in this study 256 km^2 grid cells – 1,024 km^2 grid cells), the between unit variability would be relatively low in comparison with grid cells of 16 km^2 and 64 km^2, indicating greater gamma diversity than within-habitat diversity. In this case, the smaller levels of selection unit size may be more appropriate for conservation planning.

The species richness maps and analysis of the coefficient of variation of richness also demonstrate that there does not appear to be an appropriate scale from which the variability of species richness can be predicted. Species richness appears to be highly dependent upon the size of the selection unit at which it is measured (Allen and Starr 1982).

6.4.2 Priority Biodiversity Sites

The varied location of priority biodiversity sites between level of selection unit size emphasises how scale can influence conservation decision-making. There does not appear to be one "right" level of selection unit size and the location of sites cannot be predicted from a smaller selection unit size. These results differ from a study by Davis and Stoms (1996) using only vertebrate data in California. When the resolution of the grid cell was increased, Davis and Stoms (1996) found the location of priority biodiversity site in generally the same areas. The differences in studies may be due to different methodologies in calculating priority areas (this study used summed irreplaceability) and by lack of alternative scenarios in the Davis and Stoms (1996) study. The data presented here also cover animal taxa and plant taxa, whereas the Davis and Stoms (1996) only covered vertebrates.

The efficiency by which all species can be represented at least three times is encouraging from a conservation planning perspective. Except at the largest of selection unit sizes, all species could be represented at least three times in less than 15 % of the total land in Guyana. The efficiency with which all species could be represented was higher for smaller selection units than larger ones. This finding is consistent with a similar study on efficiency by Pressey and Logan (1998). Pressey and Logan (1998) found that the efficiency of larger selection units was lower because some of the features were represented above the specified target. In the case of Guyana, the total area required varied drastically from 344 km^2 for a selection units size of 16 km^2 to 200 times that amount for a selection unit at a size of 16,384 km^2. In comparison, the efficiency of representing each species in Guyana is more than half that of Eramus *et al.* (1999) study of 199 mammal species in South Africa where they required approximately 20 % of the land to represent each species at least once using a grid cell size of 625 km^2.

6.4.3 Cross-Taxon Congruency

As discussed above, the results on cross-taxon congruency demonstrate that the effectiveness of one taxonomic group to act as a surrogate for another is dependent upon the size of the selection unit at which it is measured. At a selection unit size of 256 km^2 and smaller, the ability of different taxonomic groups to perform as surrogates appears to be based on underlying biogeographic patterns and common ecological requirements, whereas at larger selection units, the reduced number of grid cells, each containing a high portion of the total species in each taxonomic group, influences the performance of groups to act effectively as surrogates.

Further studies need to be carried out using data from other localities to determine if the effects of selection unit size are similar in other places or are particular to Guyana and the biogeography of species that have evolved on the Guiana shield. If the distribution of species across the Guiana shield is unique and this is reflected in the patterns of surrogacy observed when the size of selection units starts to capture the gamma diversity (approximately 256 km^2), then the observed patterns of species distribution may be more process-based. Common patterns of underlying biogeography and evolutionary processes depend on either the inclusion of multiple environments, each with a distinct evolutionary history as seen in the case of cross-taxon congruency patterns in the forests of Uganda (Howard *et al.* 1998), or as may be in the case of Guyana, a more homogeneous system with a spatially congruent history of speciation. These issues are important in conservation decision-making over the long-term.

If a protected area network is to be established in Guyana, it will need to conserve biodiversity as the country changes in population, economic activity and land use.

The need to understand both patterns and processes of species is paramount if priority biodiversity sites are to be conserved for the persistence and retention of species (Cowling 1999). So far, the results of this study have demonstrated that different measurements of biodiversity and different sized selection units influence the location of priority biodiversity sites in Guyana. Integrating these differences with the persistence and retention of biodiversity in light of on-going forestry and mining activities in Guyana is a challenge. Chapter seven examines one approach to trading-off the vulnerability of sites to human-induced activities with biodiversity priorities.

Chapter 7

Planning for Vulnerability, Retention and Persistence: A Protocol for Guyana

7.1 INTRODUCTION

One of the greatest challenges in conservation is planning where a network of conservation sites should be and then attempting to implement that network incrementally on the ground. Unless the entire network of sites can be conserved and managed as a network at one time, processes that destroy biodiversity will be operating while the network is being gradually implemented (sometimes over many decades). Not all features (e.g. species, vegetation classes, environmental domains) will be equally affected by the destruction or clearing of the elements of biodiversity, and thus the long-term retention of all features will depend upon integrating the vulnerability, or risk of loss, of those features into conservation planning (Dinerstein and Wikramanayake 1993, Sisk *et al.* 1994, Pressey 1997, Richardson and Funk 1999). Translating the risk of an area being cleared for logging or mining, or the encroachment of human activities into an index for conservation planning is complex. Indices of "vulnerability" can be derived to represent a measurable threat, however these indices are always oversimplifications of the potential influence anthropomorphic activities can have on biodiversity (Pressey 1997). Incorporation of the notion of vulnerability does however, provide some means for examining which sites are more likely to persist, and retain their biodiversity over time.

In previous chapters, priority biodiversity sites were identified using several measurements of biodiversity, at several different levels of scale. In this chapter, priority *conservation* sites are identified. These differ from priority biodiversity sites by incorporating some assessment of the urgency (vulnerability) with which priority biodiversity sites should be conserved. Sites that have a high biodiversity priority may have a low vulnerability index and therefore have a low overall *conservation* priority. Sites in this category might include tops of mountains, steep slopes on mountains, and remote forests. All these are "self-protecting" to some degree. On the other hand, medium priority biodiversity sites may be very threatened by human activities and be under immediate threat of losing their biodiversity. These sites would be high priority conservation sites. The "conservation value" of different sites is explored in this chapter using a combination of a derived index of vulnerability and summed irreplaceability. Two different derived indices of vulnerability are used. The first is derived from soil fertility and slope based on the premise that flat, fertile lands are the most vulnerable (compared with steep, infertile lands). The second index of vulnerability is calculated as the distance from the State Forest in Guyana that is presently under various forestry concessions. Sites within the State Forest are most vulnerable, whereas those farthest away are the least vulnerable. Priority conservation sites are identified as those with the highest summed irreplaceability and vulnerability index for a target of 3 occurrences of each species. The reduced database of 320 species used in Chapter 5 is used for these analyses. Lastly, this chapter presents a protocol for identifying priority biodiversity and conservation sites for the long-term persistence of biodiversity in Guyana. This protocol is based on the conceptual framework presented in chapter 3 and integrates results from this and previous chapters.

Although several researchers have examined the trade-offs of different sites between biodiversity and anthropomorphic activities (forestry, agriculture), they have usually adopted an approach that treats biodiversity as a commodity that can be traded-off in a cost-benefit type analysis (Faith and Walker 1996a, Faith *et al.* 1996). These approaches differ from the approach used in this chapter, as in this chapter the biodiversity priorities are considered ***in conjunction with*** an index of vulnerability. It incorporates an index on vulnerability along with an index of complementarity and biodiversity priority (summed irreplaceability). This is done using an algorithm that selects sites with the highest irreplaceability and the highest vulnerability first. The vulnerability index used here is an index of how threatened certain areas may be with regard to specific anthropogenic activities – agriculture and forestry. The approach adopted however, does not incorporate other criteria such as political and social indicators. Studies that have attempted to include these types of criteria have done so with mixed results (Mittermeier *et al.* 1998).

7.1.1. Threats to Biodiversity

The threats to biodiversity can be divided into at least two categories: threats to individual species and threats to overall biodiversity. Threats to individual species are usually due to anthropomorphic activities such as over-hunting, habitat loss and human-related uses (e.g. medicinal, decorative) (IUCN 1996). Species threatened by these types of activities are categorised as "vulnerable, threatened or endangered" (IUCN 1996). The threat status of most vertebrates and some plants is documented in the IUCN Red Data Book that is updated regularly (IUCN 1996). Planning for the retention and long-term persistence of an endangered or threatened individual species is a different process than planning for the retention and persistence of the overall biodiversity. Planning for the first type of threat usually involves detailed population viability analyses and long-term studies on home range size, demographics and minimum population sizes (Soule 1986, Shafer 1990). Threats to individual species are not considered in this chapter. Data on the status of most of the species in Guyana is not well known and only a few species are listed in the Red Book (IUCN 1996).

Threats to overall biodiversity include deforestation, increasing population density, encroachment, and economic activities such as mining, forestry and agriculture (Reyers *et al.* 1998). Several previous studies have highlighted the need to incorporate an index of threat into the designation of priority biodiversity sites. Myers's pioneering work on hotspots (1988, 1990) took into consideration both an indicator of a country's biological wealth (measured by the number of endemic plants) and an indicator of threat, which was defined as an area characterised by an exceptional threat of destruction. One drawback to Myers's approach was that the indicator of threat was determined in a wholly subjective manner. Building upon Myers's hotspots, Dinerstein and Wikramanayake (1993) identified conservation hotspots in the Indo-Pacific region using forest cover as the threat indicator and species richness and restrictedness as the biodiversity indicator. They considered a country to have a high threat indicator if the country had less than 20 % forested lands and less than 4 % of those forests were formally protected. The main drawback to this approach is that it assumes that the most important biodiversity is found in forests. This may not always be the case. Studies have shown that Mediterranean-climate areas, often lacking in trees, harbour a very high concentration of endemic plants (Cowling and Samways 1995).

Similar to the study of Dinerstein and Wikramanayake (1993), Sisk *et al.* (1994) compiled a list of global areas of 'critical concern'. These areas include countries with the highest species richness and restrictedness along with the highest annual increase in population density and annual deforestation (Sisk *et al.* 1994). However, only 7 of the 18 areas of critical concern overlap with Myers' hotspots (1988, 1990) (Sisk *et al.* 1994). A more recent study used a multivariate approach to assess the biodiversity risk of nations (Reyers *et al.* 1998). Reyers *et al.* (1998) used a stock-pressure-response framework with multiple criteria to evaluate the national biodiversity risk of 104 countries. Threat indicators (pressure indicators) included percent of land exposed to high disturbance levels, percent of threatened species, and population density (Reyers *et al.* 1998). Biodiversity indicators (stock indicators) included percent of endemic species, species density and percent of land area exposed to low disturbance levels. Response indicators included conservation budget, percent of land area protected and number of genetic resource collections. The equation of the biodiversity risk index used was: Biodiversity Risk Index = pressure indicators/ (response indicators x stock indicators) (Reyers *et al.* 1998). When conservation budgets were eliminated from the analyses (due to insufficient data), Guyana ranked 2nd lowest (after the USA) in terms of its biodiversity risk index. This was primarily due to the vast, intact forests covering most of Guyana and its extremely low population density.

All of the above analyses of threat to biodiversity were conducted at the country-level and were carried out primarily to assist funding agencies allocate limited resources to conservation projects around the world (Mittermeir *et al.* 1998). Since the driving force behind most of these studies has been the allocation of money from international aid agencies, few studies have bothered to incorporate the notion of threat when designing and planning for protected areas ***within*** a country. If, as stated previously, a systematic protected area network, designed to conserve high priority biodiversity, can only be implemented in stages over many years/decades, threats to biodiversity must be identified in order to retain biodiversity features over time. Similarly, the long-term persistence of biodiversity features may involve design considerations to protected areas that take into account pending threats.

7.1.2 Retention and Designing for Long-term Persistence of Biodiversity Features

Retention is defined here as the extent to which the features which represent biodiversity in a given area are retained after a period of simultaneous conservation action and habitat loss, regardless of whether those features of biodiversity are found within a protected area. A critical issue is the retention of both the pattern of biodiversity distribution and the ecological and evolutionary processes that maintain biodiversity (Cowling 1999). Although biodiversity features may be well represented and retained in the short-term (several decades), the long-term persistence of biodiversity, especially in light of climate change and land uses outside of formal protected areas, is difficult to plan for. Designing a protected area network for long-term persistence has not yet been tested. Only one study has examined the efficiency of a protected area network to represent known biodiversity over time, and that study only monitored changes over a 63 year period (Virolainen *et al.* 1999). Virolainen *et al.* (1999) tested the viability of the known biodiversity in Finnish lakes using reserve selection algorithms based on commonly used criteria: species richness, restricted range diversity, phylogenetic diversity and threatened species. They found that when they applied the algorithms to the data from 1933-1934 and compared it with the results obtained using data from 1996, 91 % of the phylogenetic diversity, 88 % of the original species diversity, 71 % of the threatened species and 68 % of the restricted range diversity persisted over the 63 years. A relevant conclusion from this study is that in order to maximise the viability or persistence of biodiversity over time, the selection of conservation sites should not be based on the results of one index of biodiversity using one method of selection, but rather sites should be selected based on a comparison of different methods and indices (Virolainen *et al.* 1999). The cause of loss of biodiversity was not examined in Virolainen *et al.*'s (1999) study, thus it is difficult to predict whether further loss will occur over time or whether the retention of biodiversity as measured in 1996 will remain constant.

Studies in New South Wales, Australia and the Cape Floristic Region, South Africa have attempted to incorporate a measure of vulnerability into the designation of priority conservation sites (Pressey *et al.* 1996, Cowling *et al.* 1999). The two areas face different threats. The forests of New South Wales are under threat from logging, and clearing for grazing (Pressey *et al.* 1996), whereas the Succulent Karoo of the Cape Floristic Region is primarily a desert and is under threat from overgrazing, desertification, agriculture and mining (Cowling *et al.* 1999). When an index of vulnerability to clearing is applied and used with an index of irreplaceability in the case of New South Wales, the priority of conservation sites shifts to those with the highest vulnerability to clearing and highest irreplaceability from those with the highest irreplaceability only (Pressey 1997). In this case, in order to be able to protect some of the highest priority conservation sites, management will have to occur "off-reserve", and in particular, on private lands. The feasibility and likelihood that this will occur has to be factor into any model of retention and persistence. In the case of the Succulent Karoo, achievement of any conservation goal for retention and persistence of biodiversity and the protection of key conservation sites will also require off-reserve management in addition to formal protected areas. The steps taken in the Succulent Karoo to incorporate threats while planning for retention and persistence include (Cowling *et al.* 1999):

1. Identification of types, patterns and rates of threatening processes;
2. Identification of natural features to be protected;
3. Setting quantitative targets for representation;
4. Laying out options for achieving representation;
5. Locating potential conservation areas to achieve representation; and
6. Implementing conservation actions in priority order.

In the Succulent Karoo where overgrazing and mining are the largest threats, implementing these steps to maximise the retention of priority biodiversity sites requires the establishment of three new protected areas in an area that already contains six protected areas with cover only 2.1 % of the land.

In the case of Guyana, there are several threats to biodiversity, namely logging and mining. Logging is much more of an immediate threat than mining that is presently restricted to rivers. However, the situation in Guyana is rare in that there still exists vast tracts of near pristine forest, with a very low population density and priorities for conservation sites have not yet been determined. This rare situation requires all options for achieving proper representation of Guyana's biodiversity to be explored, while considering present and future threats. This chapter adopts an approach that strives to select sites that are the most irreplaceable and the most vulnerable first. Another approach has been to treat biodiversity and its threats as a cost-benefit type curve and select sites based on an optimum on the curve (Faith *et al.* 1996).

7.1.3 Trade-offs between Biodiversity and Other Economic Activities

McNeely (1996) argued that economic value should be considered as an important criterion in the valuation of biodiversity. He argued that when the reason for biodiversity conservation was human utility, sites with the highest potential economic value (in terms of the return on their biodiversity) should be given the greatest priority. Thus, a priority conservation site could be identified based on the economic value of the resources it protects. If a dollar value could be assigned to the biodiversity at a given site then a simple trade-off curve with competing economic activities could be undertaken. Unfortunately, attempts to assign monetary values to the given biodiversity at a site fall very short of any meaningful analyses, as the market value of most biodiversity features is unknown (McNeely 1996), and by and large, it is not for market value that conservation actions are initiated.

Another approach has been to turn the problem around and view a competing activity such as forestry as a potential loss of revenue for an area when biodiversity is protected. Faith *et al.* (1996) and Faith and Walker (1996a,b) have explored the trade-offs between forgone biodiversity protection and forgone forestry opportunity in a production forest in Australia. In this approach, a trade-off curve is generated. A decision must be made at which point on the curve that the optimum exists where the forgone biodiversity protection and the forgone forestry opportunity are acceptable to the parties involved in protecting biodiversity. The advantage of this approach is that biodiversity features are treated as tradeable commodities and the loss of features can be measured. The main drawback and criticism is that it does not prioritise sites based on their relative importance in terms of biodiversity *first* and then trade off sites that are not as important in terms of their biodiversity. In contrast, the approach adopted in this study uses irreplaceability as a measure of importance for biodiversity. Sites that are completely irreplaceable (irreplaceability value of 100%) are recommended for protection outright. Sites that have an irreplaceability value of less than 100% can be traded for other uses as long as the features found within those sites can be found and protected elsewhere. This study goes one step further by adding in an index of vulnerability to ensure that the sites that are completely irreplaceable are protected, and the sites that are extremely vulnerable and irreplaceable get the highest conservation priority.

7.2 METHODS

Two indices of vulnerability were calculated for Guyana. One based on slope and soil fertility and the other on proximity to State Forests already being cleared for logging. Threats that might figure prominently in other countries, such as roads and settlements are primarily confined to a narrow strip of coast and do not pose a serious threat to Guyana's biodiversity. The examination of vulnerability and high priority biodiversity (irreplaceability) sites was done using the reduced dataset presented in Chapter 5 and summed irreplaceability to measure biodiversity. A selection unit size of 8 km x 8 km (64 km^2) was used. This selection unit size was chosen because using the selection units sizes derived in this study, 64 km^2 was the minimum size a conservation site in Guyana could be to maintain viable populations of species. Results from Chapter 6 demonstrated that there was a slight loss of variance in species richness from 16 km^2 to 64 km^2, however the patterns of cross-taxon congruency were mostly consistent.

7.2.1 Vulnerability Index based on Slope and Soil Fertility

An index of vulnerability was derived using differences in the slope and soil fertility in Guyana. The slope was calculated from the DEM presented in Chapter 4 using Spatial Analysis (1.1 ESRI 1998) in Arcview (3.1 ESRI 1998). The slope calculations were divided up into three categories. These categories were: a) $>15^o$ slope (steep); b) $10\text{-}15^o$ slope (intermediate); c) $<10^o$ slope (flat). The soil fertility map presented in Chapter 4 was used. Three categories of soil fertility were used:

a) least fertile; b) moderately fertile; and c) most fertile. In total, 9 combinations of slope and soil fertility were possible. Vulnerability was scored on a scale of 2-6 with the steepest, least fertile grid cells as the least vulnerable (index of 6) and the flattest, most fertile as the most vulnerable (index of 2) (Table 13) (Figure 41).

Table 13 - Ranking of Vulnerability Index based on Slope and Soil Fertility

Combination	**Ranking**
Steep slope, least fertile soil	6
Steep slope, moderately fertile soil	5
Steep slope, most fertile soil	4
Intermediate slope, least fertile soil	5
Intermediate slope, moderately fertile soil	4
Intermediate slope, most fertile soil	3
Flat slope, least fertile soil	4
Flat slope, moderately fertile soil	3
Flat slope, most fertile soil	2

7.2.2 Vulnerability Index based on Proximity to State Forests

The boundaries of the State Forest in Guyana currently under lease for logging are in the process of being expanded. For the purposes of this chapter, only the boundaries of the existing State Forest were used (Figure 3, chapter 2). The expansion of the State Forest will alter the results, however the Government has yet to release the definitive boundaries of the expansion. The vulnerability index based on proximity to existing State Forests was calculated as the proximity of a grid cell to the State Forest (existing forestry concessions). The vulnerability index varied from 1-304 to reflect the distance of a grid cell from the State Forest, with a value of 1 indicated that the cell was within the State Forest and a value of 304 indicated the maximum distance from the State Forest.

7.2.3 Selection of Priority Conservation Sites

Priority conservation sites were selected using minimum set algorithms built in C-Plan (see Chapters 4 and 5 for a more detailed description). The indices of vulnerability were imported into C-Plan. In this instance, sites were selected to minimise the vulnerability index and maximise their summed irreplaceability index. Summed irreplaceability was calculated using the reduced dataset of 320 species. An algorithm was run using the highest summed irreplaceable and the most vulnerable sites as the highest priority for selection. The stopping rule (target) was 3 occurrences of each species in the dataset. The algorithm was run using both indices of vulnerability. The resulting maps of priority conservation sites were produced and compared. The percent overlap using the different indices of vulnerability was compared using the Jaccard coefficient.

7.3 RESULTS

7.3.1 Vulnerability Index based on Slope and Soil Fertility

The map of the most vulnerable grid cells in Guyana shows the flat, fertile sites around Georgetown, and in the middle-east of the country as the most vulnerable (Figure 41). The central, lowland forests (primarily Greenheart) in the centre of the country are moderately vulnerable, as well as the New River Triangle area in the south-east of the country. The Pakaraima Mountains (Tepui forests) and Kanuku Mountains are the least vulnerable sites, based on this index.

7.3.2 Priority Conservation Sites based on a Vulnerability Index derived from Slope and Soil Fertility and Summed Irreplaceability

The map combining summed irreplaceability and vulnerability derived from slope and soil fertility is shown in Figure 42. When these indices are combined, the highest priority sites are found around Georgetown, in the southern savannas, in

Figure 41: Vulnerability Index based on Soil Fertility and Slope

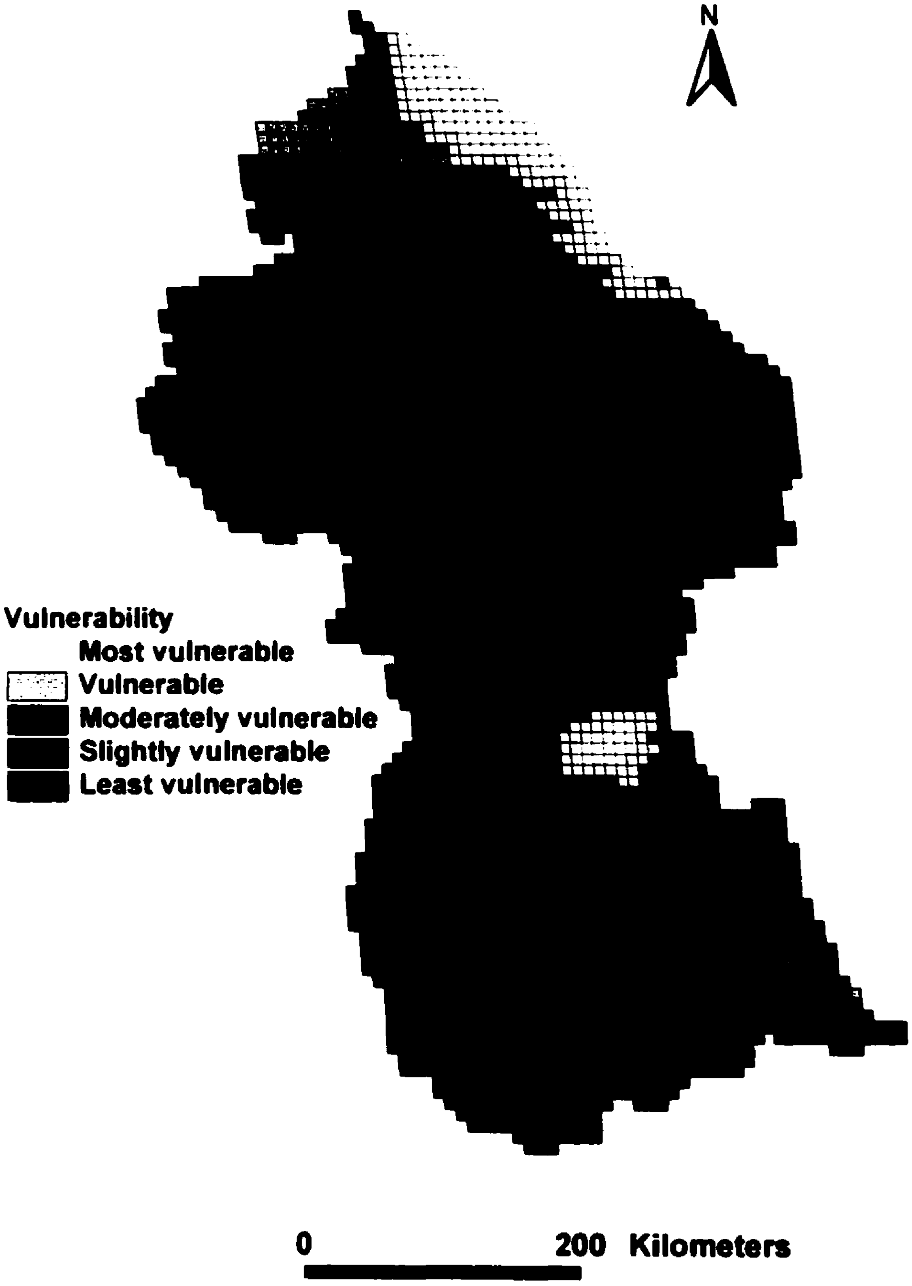
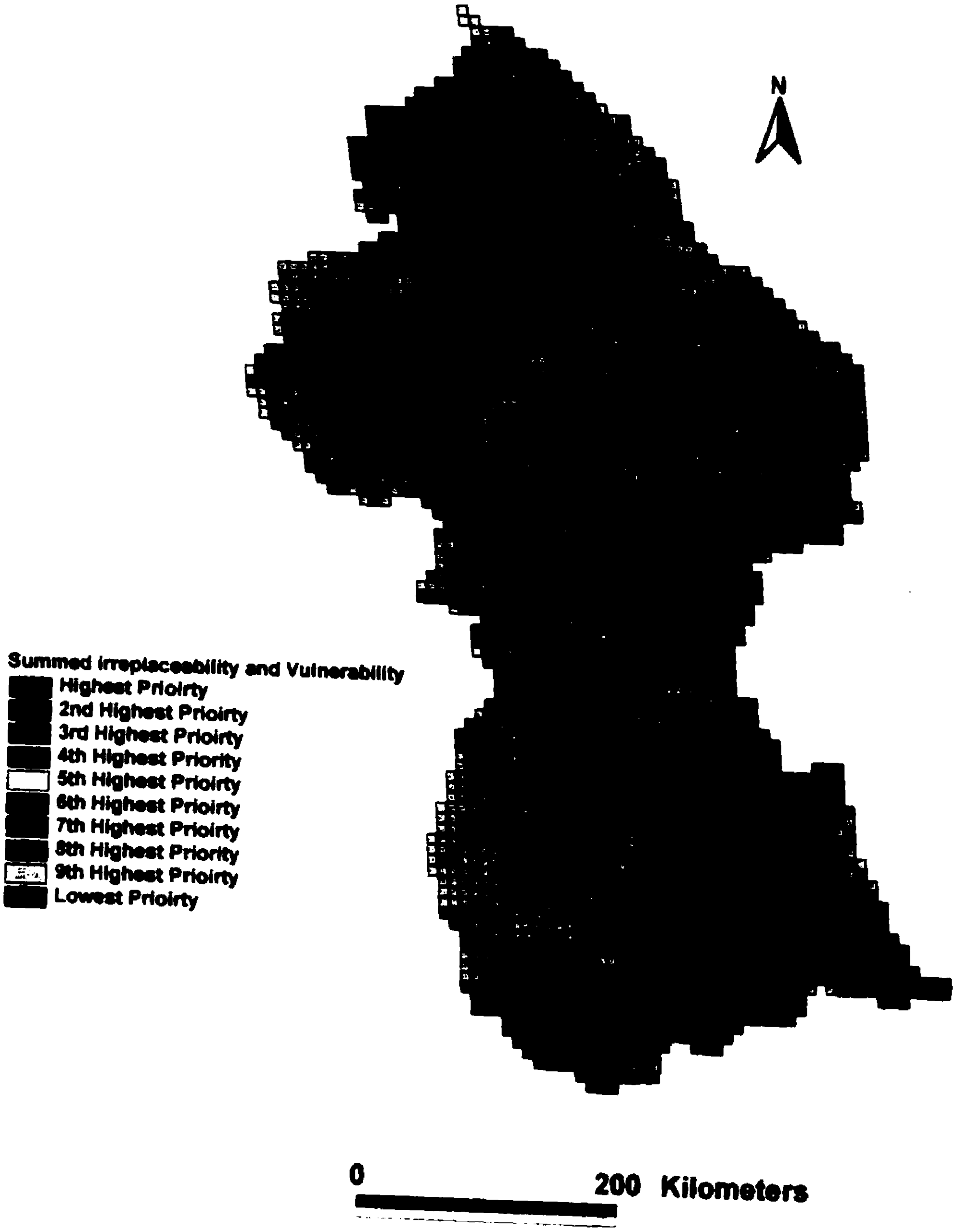


Figure 42: Ranking of Grid Cells based on Summed Irreplaceability and Vulnerability Derived from Soil Fertility and Slope



the south-east corner (New River Triangle region) and scattered throughout the central, lowland Greenheart forests and the Pakaraima Mountains. When a minimum set algorithm is used to select sites to capture each species 3 times, 631 sites are required to capture each species at least 3 times (Figure 43). The priority conservation sites are concentrated in the Pakaraima Mountains, throughout the central and eastern sections of Guyana, and one in the southern savannas (Figure 45).

7.3.3 Vulnerability Index based Proximity to the State Forest

The map of the most vulnerable grid cells based on proximity to the State Forest shows the most vulnerable sites to be within the State Forest and immediately surrounding it (Figure 44). The least vulnerable sites are in the southern savannas and the New River Triangle area.

7.3.4 Priority Conservation Sites based on a Vulnerability Index derived from the Proximity to the State Forest

The map combining summed irreplaceability and vulnerability based on proximity to State Forest is shown in Figure 45. When these indices are combined, the highest priority sites are found in the State Forests and adjacent to the State Forest.

When a minimum set algorithm was used to select sites, 285 sites were required to capture each species at least 3 times (Figure 46). The priority conservation sites were concentrated in the central and eastern part of Guyana, with a few sites along the north-eastern coast (Figure 46).

Figure 43: Selected Priority Sites based on Summed Irreplaceability and Vulnerability Derived from Soil Fertility and Slope

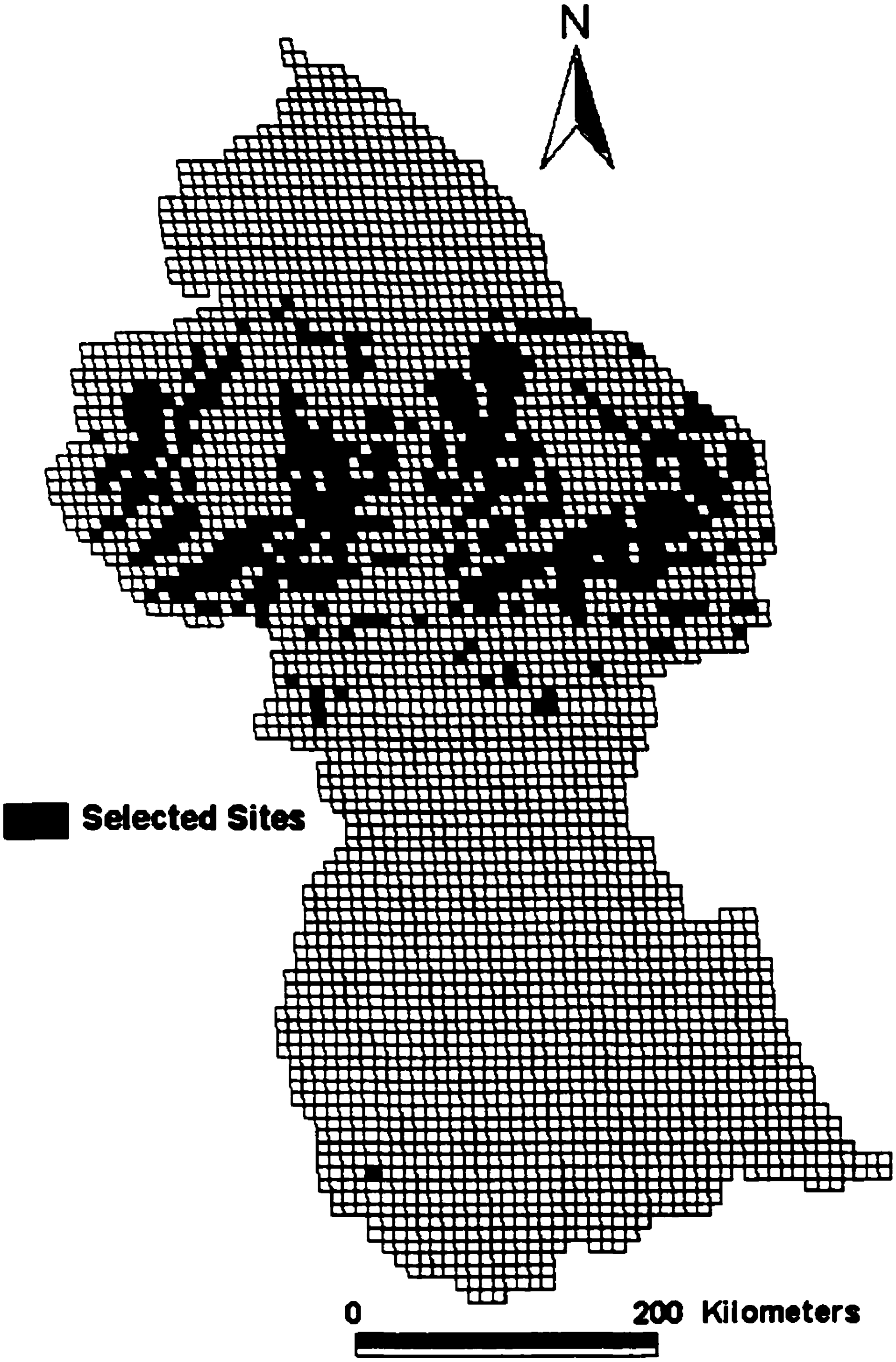


Figure 44: Vulnerability Index based on Proximity to State Forest

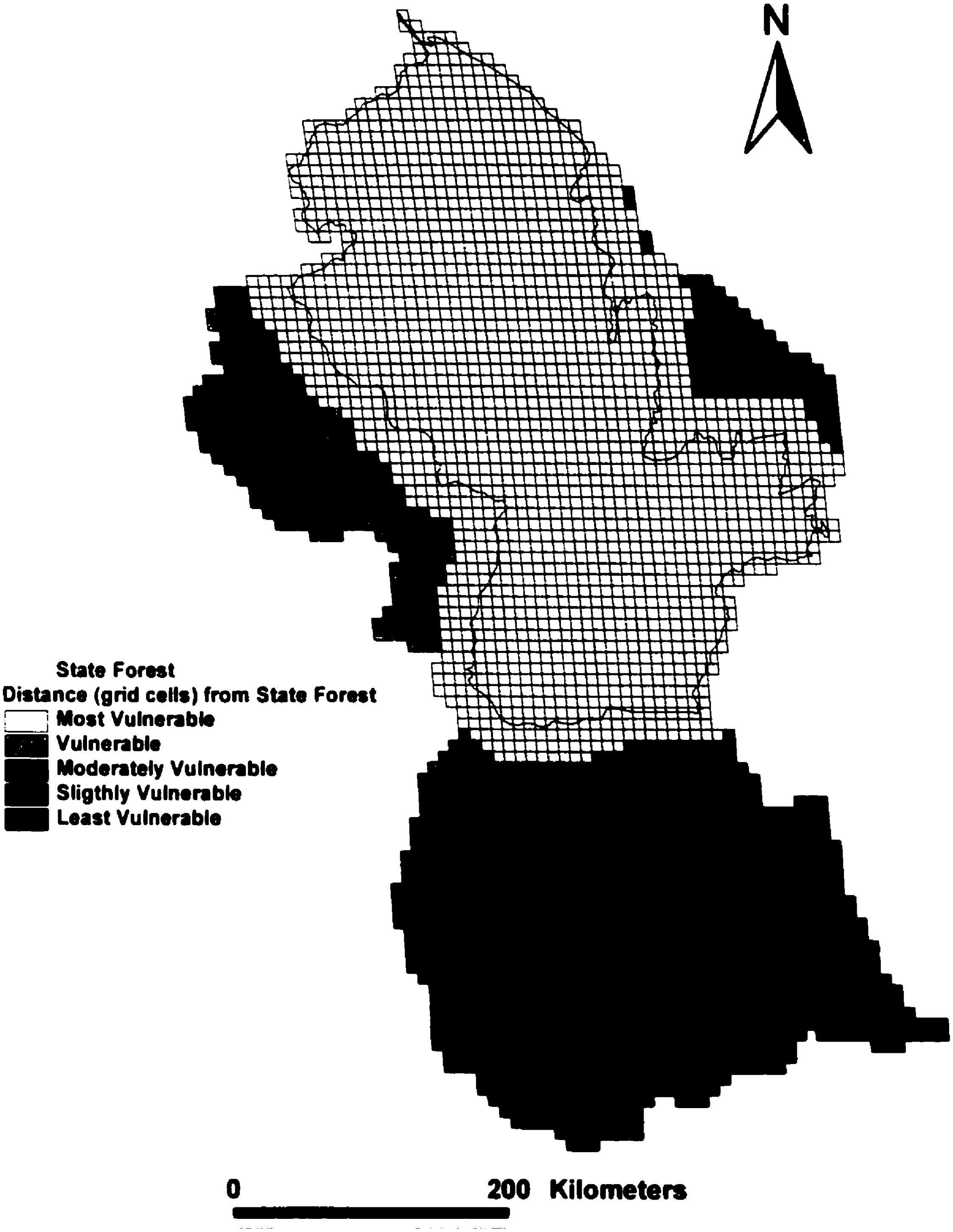


Figure 45: Ranking of Grid Cells based on Summed Irreplaceability and Vulnerability due to Proximity to State Forest

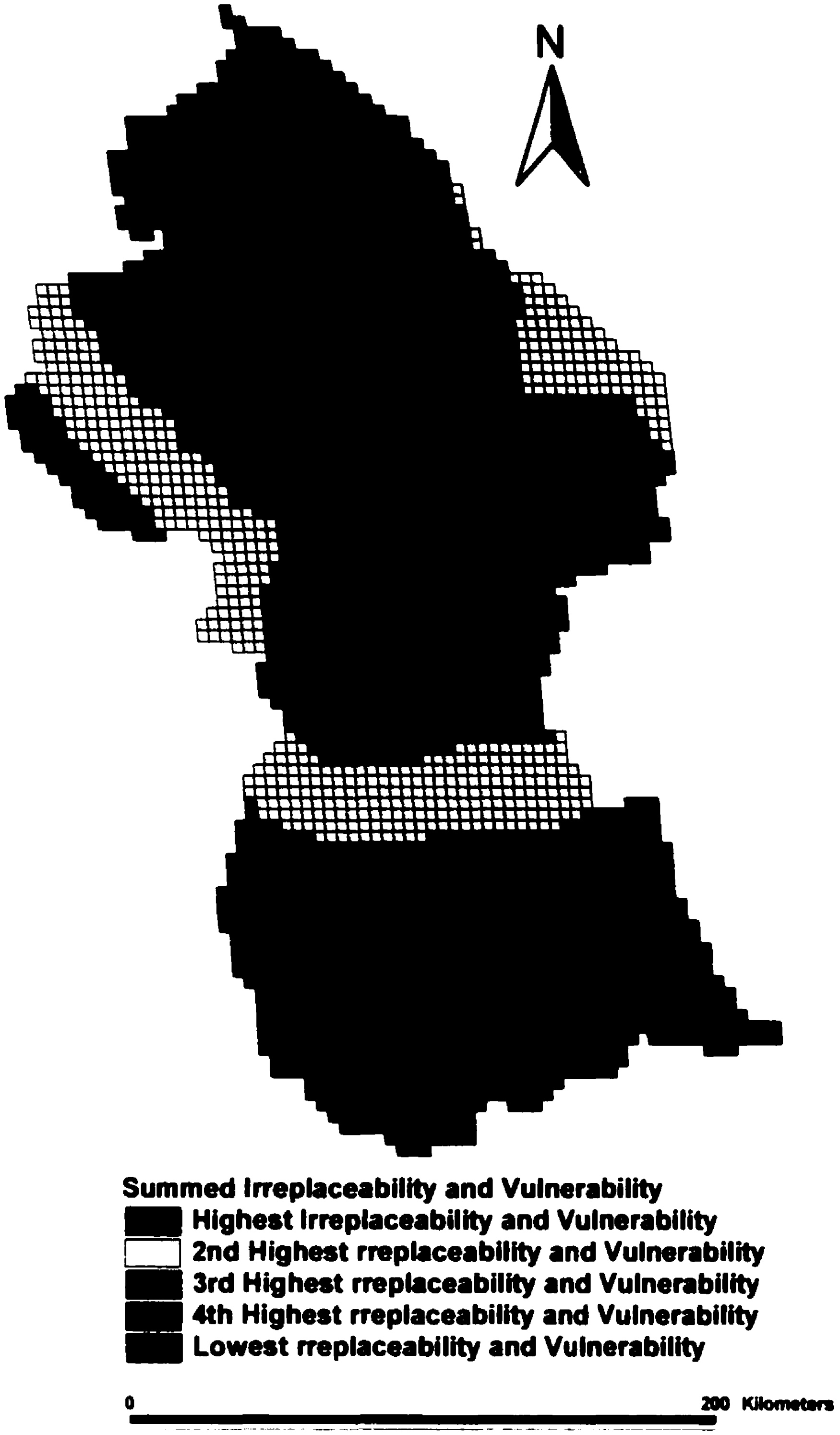
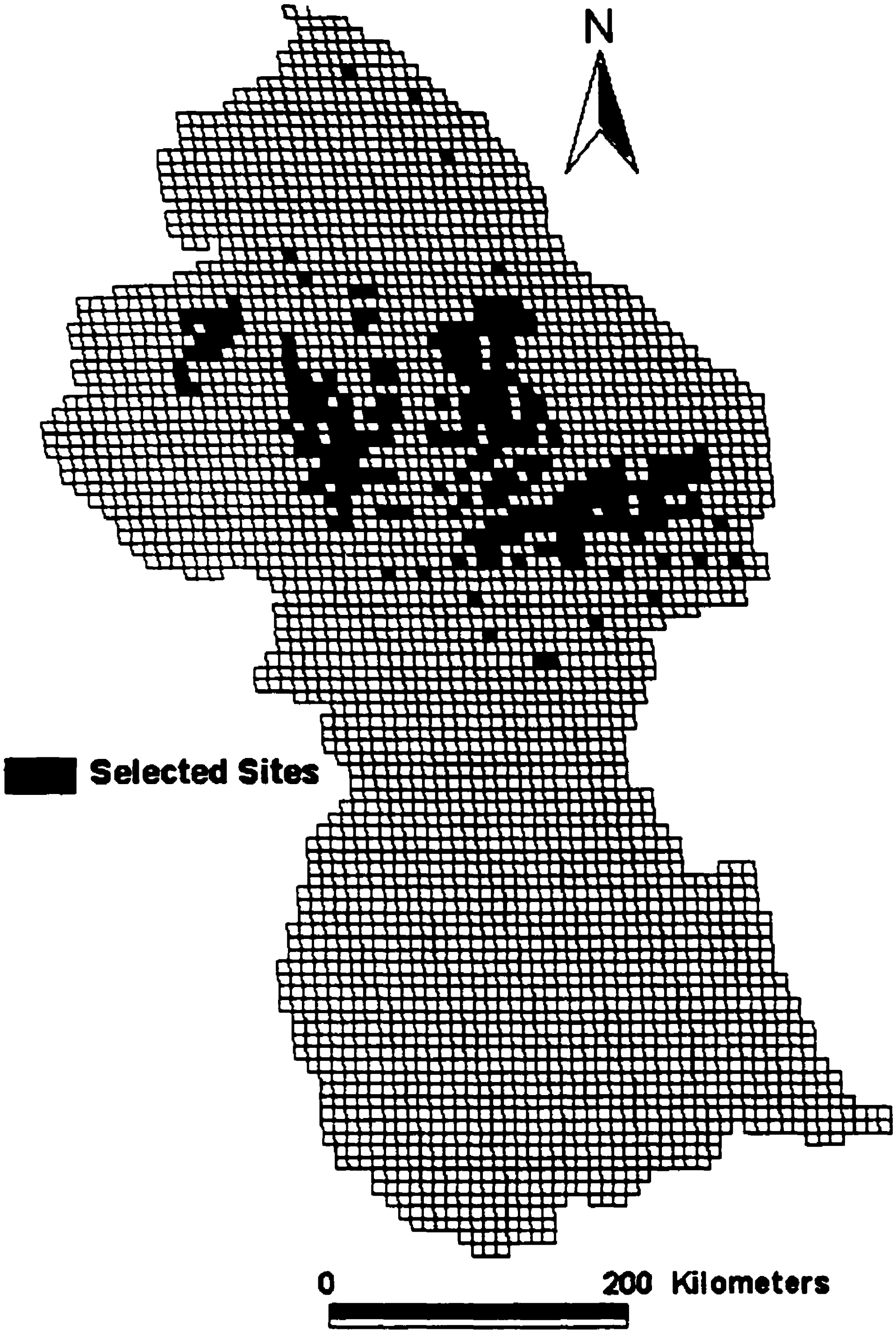


Figure 46: Selected Priority Sites based on Summed Irreplaceability and Vulnerability due to Proximity to State Forest



7.3.5 Overlap in Priority Conservation Sites

The overlap between conservation sites selected using the two different indices of vulnerability was 65.07 % (Jaccard coefficient). This relatively high degree of overlap is not surprising considering that the State Forest covers some of the flattest and most fertile land in Guyana.

7.4 DISCUSSION

Guyana is still in the rare position of having many options on how and where to conserve its biodiversity. These options are, however, disappearing rapidly as competition for land use increases with the demand for economic development. Using simple indices of vulnerability that incorporate some of the on-going threats to biodiversity in Guyana, this chapter shows that the location of priority *conservation* sites (at one spatial scale) differs significantly from the location of priority *biodiversity* sites. When sites were selected using similar selection algorithms, the minimum set required to represent the priority biodiversity was approximately 1/10 the number of sites required to represent the same biodiversity when an index of vulnerability was added. This suggests that for Guyana, options for conserving priority biodiversity are diminishing and become harder to attain as competing activities (e.g. logging and mining) increase. The results of this and previous chapters have demonstrated that there are several different solutions to protecting "priority" biodiversity in Guyana. The solutions depend upon: a) how biodiversity is measured (environmental domains, versus vegetation classes and species); b) the desired representation targets; c) the scale at which biodiversity is measured; and d) whether threats to that biodiversity are incorporated. The "real-world" solution may be none of the scenarios presented in this study, due to political, social and economic variables that are beyond the scope of this study. However, the protocol presented here could be applied to establish a real-world network of protected areas in Guyana. The conceptual framework and procedures followed in this study are flexible enough to allow for sites that are not available for conservation to be excluded from the selection procedure. These sites may include Amerindian lands, parts of the State Forest, mining sites, border areas in dispute, private land and other crown land that is currently under review for other activities.

7.4.1 Protocol for Retention and Persistence of Biodiversity in Guyana

The establishment of a protected area network in Guyana that is representative of the known biodiversity and is designed to retain that known biodiversity in the long-term, is a goal of the Government of Guyana. The real world constraints of this goal include financial restrictions (very limited budget to manage protected areas) and competing land uses (present and future). The concept of irreplaceability (Pressey *et al.* 1994) was developed to explicitly define priority for representative sites of biodiversity. In its simplest form, irreplaceability provides a measure of the likelihood that a site will be needed to achieve a conservation goal. When irreplaceability is used alone to select priority biodiversity sites in Guyana, various representative maps were produced. These maps show the most important or "irreplaceable" sites according to the target and data used. Although useful for comparative purposes, using representativeness alone does not necessarily assist a Government with planning a protected area network that encompasses all of its biodiversity and allows for the long-term persistence of that biodiversity.

In order to plan a protected area network, threats to biodiversity must be incorporated. In addition, and where possible, if there is a choice of sites between those sites deemed less irreplaceable, then choices should be made available to the Government for the situation where conservation sites need to be traded off with sites destined for other activities. This is where the principles of complementarity and irreplaceability allow for flexibility in the design of a protected area network. If there are implementation constraints (e.g. budgetary or personnel), and the Government adopts a gradual approach to implementing a protected area network, (*i.e.* protected areas are added, gazetted and managed over several decades), then it is critical that a protocol be in place that allows for the re-evaluation of the sites not yet conserved within the network. Over time, these sites may need to be re-evaluated in terms of the urgency and priority to conserve them to allow for the retention and persistence of both pattern and process of biodiversity when ongoing loss or degradation of habitat are considered (Cowling 1999).

It has been argued that the selection of protected areas should not be based on the results of a single method but rather on a comparison of results obtained using different data and methods (Kershaw *et al.* 1995, Virolainen *et al.* 1999). The results of this study demonstrate that different datasets, different measures of biodiversity, different targets and different sizes of selection units influence the location of priority biodiversity sites. None of the different methods or datasets used in this study is necessarily better than another method or dataset – they all represent the best solution for each method or dataset, although some perform better than other in representing different measures of biodiversity (e.g. vegetation classes do not represent the known species dataset well). As stated in the introduction of this thesis, there is no agreement in the literature on which method is best. However, this study does provide a first example of using the same dataset to examine many of the different methods and selection unit sizes to identify priority biodiversity.

Given that each method and dataset produces a different set of sites, and that there is some overlap between sets of sites using different methods and datasets, the following protocol attempts to encapsulate the main findings of this study (Table 14).

Table 14 - Steps in the protocol for establishing a protected area network in Guyana

Step 1	Identify features to be protected. These may include species distributions, environmental domains, and vegetation classes. These features should represent the patterns of biodiversity, however if possible they should also represent the outcomes of ecological and evolutionary processes. A mixture of species data and environmental domains should be used. Although the environmental domains efficiently capture known species data, they are not based on any known records of species and are one step removed from known species distributions. The poor congruency of different taxonomic groups at smaller selection unit sizes suggests that as much data as possible, on as many diverse groups as possible, should be used.
Step 2	Identify the types of threats (present and future) and patterns of threats to the features to be protected. In the case of Guyana, logging, Amerindian land conflict and possible mining are the three main concerns. Since logging appears to be the greatest threat, the use of an index of proximity to State Forest seems appropriate.
Step 3	Set targets for representing the features. A target that is based on capturing known species and other features a certain number of times (e.g. 3 occurrences) allows for redundancy in the network. Occurrence targets appear to be more tangible than targets based on a percentage of features, especially when species distributions are involved.

Step 4	Determine an appropriate selection unit size and possible shape. From the results of this study, the minimum selection unit size should be 64 km^2. Protected areas smaller than 64 km^2 are too small to protect the variety of species in Guyana. Preferably, areas much larger than 64 km^2 should be protected. For Guyana, regular grid cells may not be the best unit for selection. Since the country is covered in streams and rivers, watersheds may be a more appropriate unit for selection. Watersheds will vary in size, however the average watershed is approximately 120 km^2.
Step 5	Lay out options for achieving a protected area network by applying the concepts of irreplaceability and vulnerability to the dataset of features. Maximise the retention of features by minimising the extent to which the original representation targets are compromised by habitat loss while the network is being implemented. This can be achieved by protecting the sites that are most irreplaceable and most vulnerable first. If resources are used to secure these sites first, the extent to which the targets for representation are met will be maximal.
Step 6	Locate potential sites for achieving representation with as many options as possible. In the case of Guyana, sites within the State Forest may be exchangeable with other sites so as to minimise potential loss of economic revenue. Likewise, sites in the New River Triangle may be exchangeable so as to minimise conflict along the border.

Step 7	Consider design variables that will enhance the long-term persistence of features such as size, shape, connectivity, orientation and adjacency to other protected areas. Design consideration will help minimise edge effects, assist with population viability, disturbance regimes, evolutionary processes and resilience to climate change. This study did not explicitly examine design variables and their effect on the selection of priority biodiversity and conservation sites, however for biodiversity features to persist design variable must be factored in.
Step 8	Implement the necessary actions to establish and maintain the protected area network in priority order.

This protocol could be implemented using the data already collected during this study. The Government of Guyana and other stakeholders would have to participate in the formulation of targets and threats and be amenable to the choices presented. These choices, however, would provide the best opportunity for Guyana to conserve its biodiversity.

The long-term retention and persistence of biodiversity in Guyana and other countries is dependent upon a good understanding of the biological priorities and the impending threats, however the real world applications of the principles to achieve long-term conservation of biodiversity is also very dependent upon political, social and economic factors that can only be decided upon by a wider group of stakeholders including national governments, local peoples and members of the business community. An approach to conserving biodiversity must be adopted that is systematic and transparent in dealing with both data (abiotic, biotic and threat-related) and decisions (political, social and economic). The protocol presented above embraces this approach and allows for all stakeholders to participate.

Chapter Eight

Summary and Conclusions

8.1 INTRODUCTION

Guyana is a relatively small country, sparsely populated, and rich in biological diversity. Like most countries, it is trying to strike a balance between conservation and sustainable development amidst growing economic pressures. Guyana differs from many countries however, in that it has less than 1 % of its territory in formally protected areas. The opportunities to conserve large tracts of near-pristine forest and savannah still exist, although decisions on other land uses may supersede Guyana's chance to put in place an "optimal" protected area network.

This thesis attempts to contribute to knowledge and theory on surrogate measures of biodiversity, scaling theory and the designation of protected areas to conserve biodiversity, using Guyana as the case study. In addition, this thesis provides a new understanding of the patterns of climate, terrain and substrate in Guyana and extends current knowledge on the distribution of known species using spatial modelling. Although the specific results of this thesis are applicable to Guyana, the conceptual framework, main findings, and protocol for establishing protected areas can be applied to most countries.

8.2 MAIN FINDINGS

The main findings of this thesis can be summarised by examining the results obtained in each chapter with regards to the conceptual framework laid out in chapter three. The conceptual framework is based on data-driven, efficient, flexible and transparent methodologies and the five main steps are:

1. Assess and apply the most appropriate measures of biodiversity.
2. Establish explicit criteria on how to treat the data and clear conservation targets.

3. Employ a systematic selection method that is transparent, efficient, flexible and complementary in nature and incorporates some valuation of the priority with which sites should be protected (*i.e.* irreplaceability value).
4. Determine and apply an appropriate spatial scale of analysis.
5. Incorporate evaluation mechanisms.

Each of these is discussed below.

8.2.1 Measures of Biodiversity

Three different indices of biodiversity were used in this thesis: environmental domains, vegetation classes, and recorded and modelled species distributions. These measures spanned two different levels of the biodiversity hierarchy defined by Noss (1990). The high rate of cross-level congruence of sites between environmental domains and species distributions, and to a lesser degree vegetation classes and species distribution, demonstrated that surrogate measures of biodiversity could be used as substitutes for one another in Guyana. This is encouraging from a conservation planning perspective and contributes to the debate on surrogate measures of biodiversity by providing the first test of the performance of these surrogate measures of biodiversity for the neotropics. The low level of congruence between the different environmental domain classifications and the vegetation classes (with the exception of the 34 domain classification) indicate that more studies need to be conducted on the appropriate level of division of environmental domains, and the relationship between environmental domains and vegetation classes.

Results from this study showed that the cross-taxon congruence for sites selected using summed irreplaceability, was poor to moderate at small selection units sizes (16-256 km^2). Although this finding reinforces similar results from other studies, this study used more plant taxonomic groups to test cross-taxon congruence than any of the other studies examining this relationship. In general, the distribution of plants is easier to record than that of animals which tend to move and thus, it could be hypothesised that by using plant taxonomic groups, patterns of congruency might be stronger than patterns between groups of vertebrates. When patterns of congruency were observed at smaller selection unit sizes, it was generally between plant groups that shared similar ecological requirements.

Moreover, in all instances sites selected using one taxonomic group were effective at capturing a large portion of the species in the other taxonomic groups. This is a much more important finding than the lack of congruence between sites selected using the different taxonomic groups. If a protected area network was designed using one or several of the taxonomic groups used in this study, within the first 10 sites selected, 60 % of all the other species are captured and by 13 sites 100 % of all the recorded species are captured. Future work will have to focus on testing whether this patterns holds true for other countries and regions, as it has important ramifications for conservation decision-making.

8.2.2 Criteria and Representation Targets

Several criteria were used to assess the location of priority biodiversity sites. These include representation of: a) the irreplaceability values of environmental domains; b) the irreplaceability values of vegetation classes; c) species richness; d) species restricted range values; and e) the irreplaceability values of species richness. Summed irreplaceability (the sum of the irreplaceability values at a given site for the features it contains) was shown to be an effective and efficient criterion to use to prioritise biodiversity sites. Using all of the surrogate measures of biodiversity, summed irreplaceability was able to efficiently represent all features in less than 15 % of the country. In all cases of priority biodiversity sites, a range of summed irreplaceability values was calculated from completely irreplaceable (100%) to completely replaceable (0%). This range allowed for flexibility in the selection of priority biodiversity sites using minimum set algorithms. Although different solutions using the same criteria and representation target were not demonstrated in this thesis, the solutions that were produced clearly showed sites that ranged in their irreplaceability values. When priority biodiversity sites for species richness were compared with those for summed irreplaceability for species, there was very little overlap. If the aim of a protected area network is to capture the most *different* species, then the results from this study indicate that summed irreplaceability is a far better criterion for selection than species richness. If on the other hand, the aim of a protected area network is to capture as many species as possible regardless if they are the same, then species richness as a criterion may be preferred.

Two different representation targets were used for environmental domains and vegetation classes: 15 % of each classification and 3 occurrences. Results indicated that there was very little difference in the number of grid cells required to satisfy either representation target. For species, only a target of 3 occurrences of each species was used. In theory, the number of occurrences used can be as high or as low as desired. It is important however, to build-in some redundancy in a protected area network by representing each species or classification at least more than once.

8.2.3 Minimum Set Selection Algorithms

The minimum set selection algorithms used in this thesis were heuristic, iterative algorithms that attempted to capture the most biodiversity in a set of priority biodiversity sites by selecting sites with the highest summed irreplaceability first. These algorithms provided solutions to where priority biodiversity sites should be located using each of the different surrogate measures of biodiversity. In all instances, the resulting maps of priority biodiversity sites had very little overlap, however, all minimum sets contained sites in each of the biogeographical provinces of Guyana, most of the biogeographical communities and in the Pakaraima and Kanuku Mountains.

The criterion used to prioritise sites in the minimum set algorithms, summed irreplaceability, was shown to be flexible (more than one solution for measure of biodiversity was possible), complementary in its selection of sites, transparent in terms of its repeatability by any user, and efficient in the number of grid cells required to meet the representation target. When a target of 3 occurrences was used for both coarse scale and fine scale measures of biodiversity, all domains, classes and species could be represented at least three times in less than 15 % of the total land in Guyana.

8.2.4 Appropriate Spatial Scale

Spatial scale is a very important consideration in the representation of biodiversity as measured by species richness, summed irreplaceability and the selection of priority biodiversity sites. Results clearly show that different sizes of selection units produce different results in terms of the species richness of an area, the location of priority biodiversity sites, and the efficiency of different taxonomic groups to act as surrogates for one another. At selection unit sizes below 256 km^2, the effectiveness of one taxonomic group to act as a surrogate for other groups is poor, whereas at larger selection unit sizes most taxonomic groups appear to be very effective at representing other groups. Results from this thesis also show that there does not appear to be one "appropriate' level of scale at which conservation decisions should be made. Rather, each level of scale examined here has it advantages and disadvantages. At smaller selection unit sizes (16-64 km^2), the surrogate measures of biodiversity can be represented more efficiently. At medium selection unit size (256-1024 km^2), variance is loss in species richness, however taxonomic groups are starting to be effective as surrogates for one another, and the number of grid cells needed to represent all the known biodiversity at a certain representation target is still under 15 %. At the largest selection units used in this study, known biodiversity can no longer be represented in an efficient manner, however taxonomic groups are very effective at representing each other.

8.2.5 Evaluation Mechanisms

Finally, as mentioned previously, no protected area network exists in isolation of other land uses. If measurements of the degree to which priority biodiversity sites are threatened by other land uses are incorporated, or if biodiversity can be "valued" so that a trade-off of biodiversity value and other land use value can be carried out, then any protected area selection methodology needs an evaluation mechanism. This study showed that when a simple index of vulnerability was incorporated into the selection of priority sites, ten times the number of sites were needed to attain the same representation target as when threats to biodiversity were not considered. Obviously, a protected area network cannot be designed without eliminating sites that are currently under other land uses or weighting sites according to indices of priority and vulnerability. What is important, however, is that once a site is selected and actually designated as a protected area, a mechanism must be in place that allows for the continuous evaluation of threats and trade-offs so as to maximise future sites and minimise encroaching threats to existing protected areas. The protocol at the end of chapter seven presents some of the necessary steps that need to be taken to ensure the long-term persistence of biodiversity and the on-going evaluation of threats to biodiversity.

8.3 CONCLUSIONS

The aim of this thesis was to provide guidelines for the effective use of available data in the development of efficient, flexible, and practical biodiversity conservation initiatives in Guyana. This study showed that specific measures of biodiversity and specific taxonomic groups can be used as effective surrogates for biodiversity, but the scale of analysis needs to be considered. Adjacent land uses also need to be considered.

It is obvious that in a developing country, the conservation concerns of the global community may not be a high priority. The challenge for conservationists is to make clear, supportable proposals that will be compatible with realistic land use. The tools presented in this thesis should contribute. It is also important for conservationists to recognise that the cost of conservation cannot be borne fully by the country's population. External funding must be found. That too requires compelling, rational data that sets reasonable targets for conservation and can explain deliverable goals and defend expected costs. This study should help build a supportable specific case for Guyana.

Lastly, it is recognised that conservation action is often needed long before full inventories can be completed. This study should help overcome the barriers to responding to conservation needs by optimising the use that can be made of existing information. If Guyanese can move in a timely fashion to win support for conservation and generate a genuine commitment within the country, there is no reason why Guyana should not be a world leader in conservation with all of the economic, social and ethical benefits that this provides. If this can be achieved, the global conservation community will benefit by the success.

REFERENCES

Ackery, P.R. and R.I. Vane-Wright. 1984. *Milkweed butterflies, their cladistics and biology, being an account of the natural history of the Danainae, a subfamily of Lepidoptera.* Cornell University Press. New York, USA.

Adams, J.M. and F.I. Woodward. 1989. Patterns in tree species-richness as a test of the glacial extinction hypothesis. Nature 339: 699-701.

Allen, T.F.H. and T.B. Starr. 1982. *Hierarchy: Perspectives for Ecological Complexity.* University of Chicago. Chicago, USA.

Agriconsulting. 1993. *Preparatory study for the creation of protection area in Kanuku Mountains region of Guyana.* Agriconsulting. Rome, Italy.

Amersterdam, D. 1997. Tropical forest degradation: Global and Guyanese perspectives. In: Williams, P.E., J.T. Parry and M.J. Eden (eds.) *Land use, land degradation and land management in Guyana.* Commonwealth Geographical Bureau. Surrey, U.K. p. 41-52

Arrhenius, O. 1921. Species and area. J. Ecol. 9: 95-99.

Austin, M. P. 1991. Vegetation theory in relation to cost-efficient surveys. In: C. R. Margules, and M. P. Austin (eds.) *Nature Conservation: Cost Effective Biological Surveys and Data Analysis.* CSIRO. Melbourne, Australia. p.15-34.

Austin, M.P., R.B. Cunningham, and P.M. Fleming. 1984. New approaches to direct gradient analysis using environmental scalars and statistical curve-fitting procedures. Vegetatio. 55:11-27.

Austin, M. P., A. O. Nicholls, M. D. Doherty, and J. A. Meyers. 1994. Determining species response functions to an environmental gradient by means of a b-function. J.Veg. Sci.5: 215-228.

Austin, M. P., and L. Belbin. 1982. A new approach to the species classification problem in floristic analysis. Aust. J. Ecol. 7: 75-89.

Austin, M.P. and C.R. Margules. 1986. Assessing representativeness. In: M.B. Usher (ed.) *Wildlife Conservation Evaluation.* Chapman and Hall. London, U.K. p. 45-67.

Balmford, A. 1998. On hotspots and the use of indicators for reserve selection. Trends Ecol. Evol. 13:409.

Balmford, A., M. J. B. Green, and M. G. Murray. 1996a. Using higher-taxon richness as a surrogate for species richness: I. Regional tests. Proc. R. Soc. Lond. B. 263:1267-1274.

Balmford, A., A. H. M. Jayasuriya, and M. J. B. Green. 1996b. Using higher-taxon richness as a surrogate for species richness: II. Local applications. Proc. R. Soc. Lond. B. 263:1571-1575.

Bedward, M., R. L. Pressey, and D. A. Keith. 1992. A new approach for selecting fully representative reserve networks: addressing efficiency, reserve design and land suitability with an iterative analysis. Biol. Conserv. 62:115-125.

Belbin, L. 1991. Semi-strong hybrid scaling, a new ordination algorithm. J.Veg. Sci. 2:491-496.

Belbin, L.1992. Comparing two sets of community data: A method for testing reserve adequacy. Austr. J. Ecol. 17:255-262.

Belbin, L.1993a. Environmental representativeness: Regional partitioning and reserve selection. Biol. Conserv. 66:223-230.

Belbin, L., 1993b. PATN User's Manual. Canberra, Australia.

Belbin, L. 1995. A multivariate approach to the selection of biological reserves. Biodiversity and Conservation 4:951-963.

Bibby, C.J., N.J. Collar, M.J. Crosby, M.F. Heath, C. Imboden, T.H. Johnson, A.J. Long, A.J. Stattersfield, and S.J. Thirgood. 1992. *Putting Biodiversity on the Map: Priority Areas for Global Conservation.* International Council for Bird Preservation (ICBP). Cambridge, England

BioRap Consortium. 1996. Rapid assessment of biodiversity: Volume two – Tools for spatial modelling. CRES-Australian BioRap Consortium. Canberra, Australia.

Boggan, J., V. Funk, C. Kelloff, M. Hoff, G. Cremers, and C. Feuillet, 1997. *Checklist Of The Plants Of Guyana.* Biological Diversity of the Guianas Program, Department of Botany, National Museum of Natural History, Smithsonian Institution. Washington,USA.

Brooks, D.R., R.L. Mayden and D.A. McLennan. 1992. Phlogeny and biodiversity:conserving our evoutionary legacy. Trends Ecol. Evol. 7:55-59.

Burley, F.W.1988. Monitoring biological diversity for setting priorities in conservation. In: E. O. Wilson (ed.) *Biodiversity*. Washington, D. C., National Academy Press, p. 227-230.

Busby, J. R.1986. A biogeoclimatic analysis of *Nothofagus cunninghamii* (Hook.) Oerst. in southeastern Australia. Austr. J. Ecol. 11:1-7.

Busby, J.R. 1991. BIOCLIM- a bioclimate analysis and prediction system. In: C.R. Margules and M.P. Austin (eds.) *Nature Conservation: Cost effective biological surveys and data analysis*. CSIRO. Melbourne, Australia. p. 64-68.

Butterfield, B. R., B. Csuti, and J. M. Scott. 1994. Modeling vertebrate distributions for gap analysis. In: R. I. Miller (ed.) *Mapping the Diversity of Nature*. Chapman & Hall. London, UK. p. 53-68.

Caicco, S.L., J. M. Scott, B.R. Butterfield, and B. Csuti. 1995. Gap analysis of the management status of the vegetation of Idaho. Conserv. Biol. 9: 498-511.

Camm, J. D., S. Polasky, A. Solow, and B. Csuti. 1995. A note on optimal algorithms for reserve site selection. Biol. Conserv.78: 353-355.

Carpenter, G., A. N. Gillison, and J. Winter. 1993. DOMAIN: a flexible modelling procedure for mapping potential distributions of plants and animals. Biodiversity and Conservation 2: 667-680.

Ceballos, G. and J.H. Brown. 1995. Global patterns of mammalian diversity, endemism, and endangerment. Conserv. Biol. 9: 559-568.

Church, R. L., D. M. Stoms, and F. W. Davis. 1996. Reserve selection as a maximal covering location problem. Biol. Conserv. 76: 105-112.

Clark University. 1997. Idrisi Version 2.0. Idrisi Productions. Worcester, USA.

Colinvaux, P.1986. *Ecology*. John Wiley & Sons. Toronto, Canada.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. Science 199:1302-1310.

Connell, J.H. 1987. Maintenance of species diversity in biotic communities. In: S. Kawano, J. Connell, and T. Hidaka (eds.) *Evolution and Coadaptation in Biotic Communities*. University of Tokyo Press. Tokyo, Japan. p. 201-218.

Connell, J.H. and E. Orians. 1964. The ecological regulation of species diversity. Am. Nat. 98: 399-414.

Connor, E.F. and E.D. McCoy. 1979. The statistics and biology of the species area relationship. Am. Nat. 113:791-833.

Conservation International (CI). 1993. A biological assessment of the Kanuku Mountain region of southwestern Guyana. Conservation International. Washington, USA.

Cowling, R.M. 1999. Planning for persistence-systematic reserve design in southern Africa's Succulent Karoo desert. Parks. 9:17-30.

Cowling, R. M. and M.J. Samways. 1995. Predicting global patterns of endemic plant species richness. Biodiversity Letters. 2: 127-131.

Cowling, R.M., P.W. Rundel, P.G. Desmet, and K.J. Esler. 1998. Extraordinarily high regional-scale plant diversity in southern Africa arid lands: subcontinental and global comparisons. Diversity and Distributions. 4:27-36.

Cowling, R.M., R.L. Pressey, A.T. Lombard, P.G.Desmet and A.G. Ellis. 1999. From representation to persistence: requirements for a sustainable system of conservation areas in the species-rich mediterranean-climate desert of southern Africa. Diversity and Distributions 5:51-71.

Csuti, B. and A.R. Kiester. 1996. Hierarchical gap analysis for identifying priority areas for biodiversity. In: J. M. Scott, T.H. Tear and F. Davis (eds.) *Gap Analysis: A landscape approach to biodiversity planning.* American Society for Photogrammetry and Remote Sensing. Maryland, USA p. 25-37.

Csuti, B., S. Polasky, P.H. Williams, R.L. Pressey,J.D. Camm, M. Kershaw,A.R. Kiester, B. Downs, R. Hamilton, M. Huso and K. Sahr. 1997. A comparison of reserve selection algorithms using data on terrestrial vertebrates in Oregon. Biol. Conserv. 80: 83-97.

Curnutt, J., J. Lockwood, H-K. Luh, P. Nott and G. Russell. 1994. Hotspots and species diversity. Nature 367: 326-327.

Currie, D. J. and V. Paquin. 1988. Large-scale biogeographical patterns of species richness of trees. Nature 329: 326-327.

Currie, D.J. 1991. Energy and large-scale patterns of animal- and plant species richness. Am. Nat. 137: 27-49.

Dalfelt, A.1978. *Nature conservation survey of the Republic of Guyana.* IUCN. Costa Rica.

Darlington, P.J. 1957. *Zoogeography: The Geographical Distribution of Animals.* John Wiley and Sons. New York, USA.

Davis, F. W. and D.M. Stoms. 1996. A spatial analytical hierarchy for Gap Analysis. In: J. M. Scott, T.H. Tear and F. Davis (eds.) *Gap Analysis: A* *landscape approach to biodiversity planning.* American Society for Photogrammetry and Remote Sensing. Maryland, USA p. 15-24.

Davis, F.W., D.M. Stoms and S. Andelman. 1999. Systematic reserve selection in the USA: an example from the Columbia Plateau ecoregion. Parks. 9:31-41.

Diamond, J.M. 1973. Distributional ecology of New Guinea birds. Science 179:759-769.

Diamond, J.M. 1986. The design of a nature reserve system for Indonesian New Guinea. In: M. E. Soule (ed.) *Conservation Biology: The Science of Scarity and Diversity*, Sinauer Associate. Massachusetts, USA. p. 485-503.

Dinerstein, E. and E. D. Wikramanayake. 1993. Beyond "hotspots": how to prioritze investments to conserve biodiversity in the Indo-Pacific region. Conserv. Biol. 7: 53-65.

Dobson, A.P., J.P.Rodriguez, W.M. Roberts, and D.S. Wilcove. 1997. Geographic distribution of endangered species in the United States. Science. 275: 550-553.

DOMAIN (1997). Version 1.4 Centre for International Forestry Research. Bogor, Indonesia.

Eden, M. J.1964. *The Savanna Ecosystem: Northern Rupununi, British Guiana.* McGill University. Montreal, Canada.

Ehrendorfer, F. 1970. Evolutionary patterns and strategies in seed plants. Taxon 19: 185-195.

Eramus, B. F. N., S. Freitag, K.J.Gaston, B.H. Erasmus and A.S. Van Jaarsveld. 1999. Scale and conservation planning in the real world: Proc. R. Soc. Lond B. 266: 315-319.

Environmental Systems Research Institute (ESRI) 1998. ArcView GIS Version 3.1. Neuron Data.

Environmental Systems Research Institute (ESRI) 1998. ArcView Spatial Analyst 1.1. Neuron Data.

Faith, D. P. 1991. Effective pattern analysis methods for nature conservation. In: C. R. Margules, and M. P. Austin (eds.). *Nature Conservation: Cost Effective Biological Surveys and Data Analysis.* CSIRO. Melbourne, Australia.

Faith, D.P. and P.A. Walker. 1995. DIVERSITY: a software package for sampling phylogenetic and environmental diversity, a user's guide. CSIRO. Canberra, Australia.

Faith, D.P. and P.A. Walker. 1996a. Integrating conservation and development: effective trade-offs between biodiversity and cost in the selection of protected areas. Biodiversity and Conservation 5:431-446.

Faith, D.P. and P.A. Walker. 1996b. Environmental diversity: on the best possible use of surrogate data for assessing the relative biodiversity of sets of areas. Biodiversity and Conservation 5:399-415.

Faith, D. P., P. A. Walker, J. R. Ive, and L. Belbin. 1996. Integrating conservation and forestry production: exploring trade-offs between biodiversity and production in regional land-use assessment. Forest Ecology and Management 85: 251-260.

Fanshawe, D.B. 1952. *The vegetation of British Guiana: A preliminary review.* Imperial Forestry Institute, University of Oxford. Oxford, UK. Vol. 29.

Fanshawe, D.B. 1954. Riparian vegetation of British Guiana. J. Ecol. 42: 289-295.

Ferrier, S. 1997. Biodiversity data for reserve selection: making best use of incomplete information. In: J. J. Pigram, and R. C. Sundell (eds.) *National Parks and Protected Areas: Selection, Delimitation, and Management.* Centre for Water Policy Research. Armidale, Australia. p. 315-329.

Ferrier, S. and G. Watson. 1997. *An evaluation of the effectiveness of environmental surrogates and modelling techniques in predicting the distribution of biological diversity.* Department of Environment, Sport and Territories. Canberra, Australia

Ferrier, S., R.L. Pressey, T.W. Barrett. 2000. A new predictor of the irreplaceability of areas for achieving a conservation goal, its application to real-world planning, and a research agenda for further refinement. Biol. Conserv. In press.

Fischer, A.G. 1960. Latitudinal variations in organic diversity. Evolution 14: 64-81.

Flather, C. H., K.R. Wilson, D.J. Dean, and W. McComb. 1997. Identifying gaps in conservation networks: Of indicators and uncertainty in geographic-based analyses: Ecol. Appl. 7: 531-542.

Freitag, S. and A.S. Van Jaarsveld. 1997. Relative occupancy, endemism, taxonomic distinctiveness and vulnerability: Prioritizing regional conservation actions. Biodiversity and Conservation 6: 211-232.

Freitag, S. and A. S. Van Jaarsveld 1998. Sensitivity of selection procedures for priority conservation areas to survey extent, survey intensity and taxonomic knowledge. Proc. R. Soc. Lond B. 265: 1475-1482.

Freitag, S., A. S. Van Jaarsveld, and H. C. Biggs. 1997. Ranking priority biodiversity areas: an iterative conservation value-based approach. Biol. Conserv. 82: 263-272.

Funk, V.A., M.F. Zermoglio and N. Nassir. 1999. Testing the use of specimen based collecting data and GIS in biodiversity exploration and conservation decision-making in Guyana. Biodiversity and Conservation 8:727-751.

Gaston, K.J. 1994. *Rarity*. Chapman and Hall. London, UK.

Gaston, K.J and P.H. Williams 1996. Spatial patterns in taxonomic diversity. In: Gaston, K.J. (ed.) *Biodiversity: a biology of numbers and difference*. Blackwell Science. Oxford, UK.p. 202-229.

Gentry, A. H.1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. Ann. Missouri. Bot. Gard. 75: 1-34.

Gentry, A.H. 1992. Tropical forests biodiversity: distributional patterns and their conservational significance. Oikos 63: 19-28.

Gleason, H.A. 1922. On the relation between species and area. Ecology 3: 158-162.

Gorts-van Rijn. 1990. A.R.A. [editor]. *Flora of the Guianas*. Koeltz Scientific Books. Germany.

Guyana Agency for Health Sciences Education, Environment and Food Policy (GAHEF). 1992. Country Study of Biological Diversity. UNEP. Georgetown, Guyana.

Government of Guyana. 1991. *Census of Guyana*. Georgetown, Guyana.

Government of Guyana. 1994. *National Environmental Action Plan*. Office of the President. Georgetown, Guyana.

Government of Guyana. 1995. *Growth Indices in Guyana*. Minister of Finance. Georgetown, Guyana.

Government of Guyana 1998. *National Protected Areas System Project-working document*. Office of the President. Georgetown, Guyana.

Harrison, S.G. 1958. Botanical survey of Waranama and Ebini. Intermediate savannahs, Berbice River, British Guiana. In: Hills, T.L. (ed.) *Guyana Coastal lowlands: geography and environment*. McGill University, Montreal, Canada.

Harrison, S,. S.J. Ross and J.H. Lawton. 1992. Beta diversity on geographic gradients in Britain. J. Anim. Ecol. 61: 151-158.

Hills, T. L. (1965). Savannas: *A Review of a Major Research Problem in Tropical Geopgraphy*. McGill University. Montreal, Canada.

Hills, T. L. (1969). *The Savanna Landscapes of the Amazon Basin*. McGill University. Montreal, Canada.

Howard, P., P. Viskanic, T.R.B. Davenport, F.W. Kigenyi, M. Baltzer, C.J. Dickinson, J.S.Lwanga, R.A.Mattews, and A. Balmford. 1998. Complementarity and the use of indicator groups for reserve selection in Uganda. Nature 394: 472-475.

Huber, O., G. Gharbarran and V.A. Funk. 1995. Preliminary vegetation map of Guyana. Biological Diversity of the Guianas Program. Smithsonian Institution. Washington, USA.

Huston, M. 1979. A general hypothesis of species diversity. Am. Nat. 113: 81-101.

Hutchinson, M.F. 1989 ANUDEM Version 1.1. Centre for Environmental Studies, ANU. Canberra, Australia.

Hutchinson, M.F. 1993 ANUSPLIN Version 2.1. Centre for Environmental Studies, ANU. Canberra, Australia.

Hutchinson, M.F. 1998 ANUCLIM Version 4.0. Centre for Environmental Studies, ANU. Canberra, Australia.

Hydrometeorological Service of Guyana. 1992. Climate Records for Guyana from 1976-1988. Hydrometeorological Service of Guyana. Georgetown, Guyana.

Iwokrama. 1999. Iwokrama Centre for Rain Forest Conservation and Development. Web Page. http://www.sdnp.org.gy/iwokrama.

Kelloff, C.L. 1999. Carol Kelloff's Kaieteur Home Page. http://mason.gmu.edu/~ckelloff/index.html.

Kelloff, C.L. and V.A. Funk. 1999. *Preliminary checklist of the plants of Kaieteur National Park, Guyana*. Smithsonian Institution. Washington, USA.

Kareiva, P. and M. Andersen. 1988. Spatial aspects of species interactions: the wedding of models and experiments. In: A. Hastings (ed.) *Community Ecology*. Springer-Verlag. New York, USA. p. 38-54.

Kerr, J. T. 1997. Species richness, endemism, and the choice of areas for conservation. Conserv. Biol.11:1094-1100.

Kershaw, M., P.H. Williams, and G.M. Mace. 1994. Conservation of Afrotropical antelopes" consequences and efficiency of using different site selection methods and diversity criteria. Biodiversity and Conservation 3: 354-372.

Kiester, A. R., J. M. Scott, B. Csuti, R. F. Noss, B. Butterfield, K. Sahr, and D. White. 1996. Conservation Prioritization Using GAP Data. Conserv. Biol.10: 1332-1342.

Kikkawa, J. and E.E. Williams 1971. Altitudinal distribution of land birds in New Guinea. Search 2: 64-69.

Kirkpatrick, J.B. 1983. An iterative method for establishing priorities for the selection of nature reserves: an example from Tasmania. Biol. Conserv. 25:127-134.

Kirkpatrick, J.B. and M.J. Brown. 1994. A comparison of direct environmental domain approaches to planning reservation of forest, higher plant communities and species in Tasmania. Conserv. Biol. 70:143-147.

Landres, P.B., J.Verner, and J.W. Thomas. 1988. Ecological uses of vertebrate indicator species: a critique. Conserv. Biol. 2:316-328

Lapin, M. and B.V. Barnes. 1995. Using the landscape ecosystem approach to assess species and ecosystem diversity. Conserv. Biol. 9: 1148-1158.

Lawton, J.H., J.R. Prendergast and B.C. Eversham. 1994. The numbers and spatial distributions of species: analyses of British data. In: Forey, P.L., C.J. Humphries and R.I. Vane-Wright (eds.). *Systematics and conservation evaluation*. Clarendon. Oxford, UK. p. 177-195.

Lawton, J. H., D.E.Bignell, B.Bolton, G.F.Bloemers, P.Eggleton, P.M.Hammond, M. Hodda, R.D.Holt, T.B.Larsen, N.A Mawdsley, N.E. Stork, D.S. Srivastava, and A.D.Watt. 1998. Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. Nature 391: 72-75.

Levin, S.A.1992. The problem of pattern and scale in ecology. Ecology 73: 1943-1967.

Lindenmayer, D.B., H.A. Nix, J.P. McMahon, M. F. Hutchinson, and M. T.

Tanton. 1991. The conservation of Leadbeater's possum, *Gymnobelideus leadbeateri* (McCoy): a case study of the use of bioclimatic modelling. J. Biogeog. 18: 371-383.

Linder, H. P.1995. Setting conservation priorities: the importance of endemism and phylogeny in the southern African orchid genus *Herscheli.* Conserv. Biol. 9: 585-595.

Lombard, A. T., A. O. Nicholls, and P. V. August. 1995. Where should nature reserves be located in South Africa? A snake's perspective. Conserv. Biol. 9: 363-372.

Lombard, A. T., R. M. Cowling, R.L. Pressey and P. J. Mustart. 1997. Reserve selection in a species-rich and fragmented landscape on the Agulhas Plain, South Africa. Conserv. Biol. 11:1101-1116.

Lombard, A.T., C. Hilton-Taylor, A.G. Rebelo, R.L. Pressey, and R.M. Cowling. 1999. Reserve selection in the Succulent Karoo, South Africa: coping with high composition turnover. Plant Ecology (In press).

MacArthur, R.H. 1965. Patterns of species diversity. Biol. Rev. 40: 510-533

MacArthur, R.H. and E.O. Wilson. 1963. An equilibrium theory of insular zoogeography. Evolution 17: 373-387.

MacArthur, R.H. and E.O. Wilson. 1967. *The Theory of Island Biogeography.* Princeton University Press. Princeton, USA.

MacArthur, R.H. and J.W. MacArthur. 1961. On bird species diversity. Ecology 42: 594-598.

Mackey, B.G., H.A. Nix, M.F. Hutchinson, J.P. MacMahon and P.M. Fleming. Assessing the representativeness of places for conservation reservation and heritage listing. Environmental Management 12: 501-514.

Mackey, B.G., H. A. Nix, J. A. Stein, and S. E. Cork. 1989. Assessing the representativeness of the wet tropics of Queensland world heritage property: Biol. Conserv. 50: 279-303.

Magurran, A.E. 1988. *Ecological Diversity and its Measurements.* Princeton University Press. Princeton, USA.

Margules, C. R. and A. O. Nicholls.1988. Selecting networks of reserves to maximise biological diversity. Biol. Conserv. 43: 63-76.

Margules, C. R. and M.P. Austin. 1994. Biological models for monitoring species decline: the construction and use of data bases. Phil. Trans.R. Soc. Lond. B. 344:69-75.

Margules, C. R. and J. L. Stein.1989. Patterns in the distributions of species and the selection of nature reserves: an example from eucalyptus forests in south-eastern New South Wales. Biol. Conserv. 50: 219-238.

Margules, C.R. and T.D. Redhead. 1995. *Guidelines for using the BioRap methodology and tools*. CSIRO. Melbourne, Australia.

Margules, C.R., A.O. Nicholls and R.L. Pressey. 1988. Selecting networks of reserves to maximize biological diversity. Biol. Conserv. 43: 63-76.

Margules, C.R. and I.D. Cresswell, and A.O. Nicholls. 1994. A scientific basis for establishing networks of protected areas. In: Forey, P.L., C.J. Humphries and R.I. Vane-Wright (eds.). *Systematics and conservation evaluation.* Clarendon. Oxford, UK. p. 327-350

McConnell, R.B. and B. Choubert. 1975. Guiana Shield-Regional Survey. In: Fairbridge, R.W. [ed.]. *Encyclopedia of World Regional Geology, Part I: Western Hemisphere*. Dowden, Hutchinson, & Ross, Inc. Stroudsburg.

McNeeley, J.A. 1994. Protected areas for the 21st century: working to provide benefits to society. Biodiversity and Conservation. 3:390-405.

McNeely, J. A. 1996. Investing in biological diversity: assessing methods for setting conservation priorities: OECD International Conference on Incentive Measures for the Conservation and the Sustainable Use of Biological Diversity. Cairns, Australia.

McNeely, J.A., K.R. Miller, W.V. Reid, R.A. Mittermeier, and T.B. Werner. 1990. *Conserving the World's Biological Diversity*. IUCN. Gland, Switzerland.

Meetnemyer, V. and E.O. Box. 1987. Scale effects in landscape studies. In: M.G. Turner (ed.) *Landscape Heterogeneity and Disturbance*. Springer-Verlag. New York, USA. p. 15-36.

Meffe, G. K. and C. R. Carroll. 1994. *Principles of conservation biology*. Sinauer Associates Inc. Sunderland, USA.

Mittermeier, R.A. and T.B. Werner. 1990. Wealth of plants and animals unites "Megadiversity" countries. Tropicus. 4: 4-5.

Mittermeier, R. A., N. Myers, and J.B. Thomsen. 1998. Biodiversity hotspots and major tropical wilderness areas: Approaches to setting conservation priorities. Conserv. Biol. 12: 516-520.

Mortiz, C. 1995. Uses of molecular phylogenies for conservation. Phil. Trans.R. Soc. Lond. B. 349:113-118.

Moritz, C. and D.P. Faith.1998. Comparative phylogeograpghy and the identification of genetically divergent areas for conservation. Molecular Ecology. 7: 419-429.

Murphy, D.D. 1989. Conservation and confusion: wrong species, wrong scale, wrong conclusions. Conserv. Biol. 3: 82-87

Murphy, D.D, and B.A Wilcox. 1986. Butterfly diversity in natural habitat fragments: a test of the validity of vertebrate-based management. In: Verner, J., M.L. Morrison and C.J. Ralph (eds.). *Wildlife 2000: modeling habitat relationships of terrestrial vertebrates*. University of Wisconsin Press. Madison, USA. p. 287-292.

Myers, N. 1988. Threatened biotas: "Hotspots" in tropical forests. Environmentalist. 8: 1-20.

Myers, N. 1990. The biodiversity challenge: Expanded hot-spot analysis. Environmentalist. 10: 243-256.

Nicholls, A. O. 1989. How to make biological surveys go further with generalised linear models. Biol. Conserv. p. 51-75.

Nicholls, A. O. 1991. Examples of the use of generalised linear models in analysis of survey data for conservation evaluation. In: C. R. Margules and M. P. Austin (eds.) *Nature Conservation: Cost Effective Biological Surveys and Data Analysis*. CSIRO. Melbourne, Australia. p. 43-62.

Nicholls, A. O.and C. R. Margules. 1993. An upgraded reserve selection algorithm. Biol. Conserv.64: 165-169.

Nix, H.A. 1982. Environmental determinants of biogeography and evolution in Terra Australis. In: Baker. W.R and P.J.M. Greenslade (eds.) *Evolution of the flora and fauna of Australia*. Peacock Publishers. Adelaide, Australia. p. 47-66.

Nix, H.A. 1986. A biogeographic analysis of Australian elapid snakes. In: *Atlas of Elapid Snakes of Australia*. Australian Flora and Fauna Series. Australian Government Publishing Service. Canberra, Australia. 7:4-15.

Nix, H. A., and M. A. Switzer. 1991. *Rainforest Animals: Atlas of Vertebrates Endemic to Australian Wet Tropics*. Kowari 1.Australian National Parks and Wildlife Service Publication. Canberra, Australia.

Nix, H.A., M.F. Hutchinson, C.F. Margules, D.P. Faith, and J.West.1999. *Papua New Guinea Biorap Project-working document*. World Bank. Washington, USA.

Noss, R.F. 1983. A regional landscape approach to maintain diversity. BioScience 33:700-706.

Noss, R.F. 1987. From plant communities to landscapes in conservation inventories: a look at the Nature Conservancy (USA). Biol. Conserv. 41:11-37.

Noss, R. F. 1990. Indicators for monitoring biodiversity: A hierarchal approach: Conserv. Biol. 4: 355-364.

Noss, R.F. and L.D. Harris. 1986. Nodes, networks and MUMs: preserving diversity at all scales. Environmental Management 10:299-309.

NSW NPWS 1999. C-Plan Module. Beta 2.2 http://www.ozemail.com/~cplan.

Odum, E.P. 1989. *Ecology and our Endangered Life-support Systems*. Sinauer Associates. Sunderland, USA.

Office of Technology Assessment (OTA). 1987. *Technologies to maintain biological diversity*. US Government Printing Office. Washington, USA.

Olson, D. M. and E. Dinerstein 1998. The global 200: A representation approach to conserving the Earth's most biologically valuable ecoregions. Conserv. Biol. 12: 502-515.

O'Neil, R. V. 1996. Recent developments in ecological theory: hierarchy and scale.In: J. M. Scott, T.H.Tear, and F.Davis, (eds.). *Gap Analysis: A landscape Approach to Biodiversity Planning*. American Society for Photogrammetry and Remote Sensing. Maryland, USA. p.7-13

O'Neill, R.V., B.T. Milne, M.G. Turner, and R.H. Gardner. 1988. Resource utilization scales and landscape pattern. Landscape Ecology 2: 63-69.

O'Neil, R.V. S.J. Turner, V.I. Cullinan, D.P. Coffin, T. Cook, W. Conley, J. Brunt, J.M. Thomas, M.R. Conley, and J. Gosz. 1991. Multiple landscape scales: an intersite comparison. Landscape Ecology 5:137-144.

Owen, J.G. 1988. On productivity as a predictor of rodent and carnivore diversity. Ecology 69 1161-1165.

Owen, J. G. 1989. Patterns of herpetofaunal species richness: relation to temperature, precipitation, and variance in elevation. J. Biogeog. 16:141-150.

Owen, J. G. 1990. Patterns of mammalian species richness in relation to temperature, productivity, and variance in elevation. J. Mamm. 71:1-13.

Pearson, D. L. and F. Cassola. 1992. World-wide species richness patterns of tiger beetles (*Coleoptera: Cicindelidae*): Indicator taxon for biodiversity and conservation studies. Conserv. Biol. 6: 376-391.

Pearson, D.L. and S.S. Carroll. 1998. Global patterns of species richness: spatial models for conservation planning using bioindicator and precipitation data. Conserv. Biol. 12:809-821.

Pianka, E. R. 1966. Latitudinal gradients in species diversity: a review of concepts. Am. Nat.100: 33-46.

Pianka, E.R. 1978. *Evolutionary Ecology*. Harper and Row Publishers, New York.

Pianka, F.R. 1966. Latitudinal gradients in species diversity: a review of the concepts. Am. Nat. 100: 33-46.

Pielou, E.C. 1975. *Ecological Diversity*. Wiley. New York, USA.

Pimm, S. L.and J. H. Lawton. 1998. Planning for biodiversity. Science 279:2068-2069.

Prendergast, J. R., R. M. Quinn, B. C. Lawton, B. C. Eversham, and D. W. Gibbons. 1993. Rare species, the coincidence of diversity hotspots and conservation strategies. Nature 365: 335-337.

Prendergast, J.R., R.M. Quinn and J.H. Lawton. 1999. The gaps between theory and practice in selecting nature reserves. Conserv. Biol. 13: 484-492.

Pressey, R. L.1994. Ad hoc reservations: forward or backward steps in developing representative reserve systems? Conserv. Biol. 8:662-668.

Pressey, R. L.1997. Priority conservation areas: towards an operational definition for regional assessments. In: J. J. Pigram, and R. C. Sundell (eds.) *National Parks and Protected Areas: Selection, Delimitation, and Management*. Centre for Water Policy Research. Armidale, Australia. p. 337-357.

Pressey, R. L.1999. Applications of irreplaceability analysis to planning and management problems. Parks 9: 42-51.

Pressey, R. L. and A.O. Nicholls. 1989a. Application of a numerical algorithm to the selection of reserves in semi-arid New South Wales. Biol. Conserv. 50: 263-279.

Pressey, R. L. and A.O.Nicholls. 1989b. Efficiency in conservation evaluation: scoring versus iterative approaches. Biol. Conserv. 50: 199-217.

Pressey, R. L. and V. S. Logan. 1994. Level of geographical subdivision and its effects on assessments of reserve coverage: a review of regional studies. Conserv. Biol. 8: 1037-1046.

Pressey, R.L. and S.L. Tully. 1994. The cost of *ad hoc* reservation: a case study in western New South Wales. Aust. J. Ecol. 19:375-384.

Pressey, R. L. and V. S. Logan. 1995. Reserve coverage and requirements in relation to partitioning and generalization of land classes: analyses for western New South Wales: Conserv. Biol. 9: 1506-1517.

Pressey, R. L. and V.S. Logan. 1998. Size of selection unit for future reserves and its influence on actual v. targeted representation of features: A case study in western New South Wales. Biol. Conserv. 85: 305-319.

Pressey, R. L., I. R. Johnson, and P. D. Wilson. 1994. Shades of irreplaceability: towards a measure of the contribution of sites to a reservation goal. Biodiversity and Conservation. 3: 242-262.

Pressey, R. L., H. P. Possingham, and C. R. Margules. 1995. Optimality in reserve selection algorithms: when does it matter and how much? Biol. Conserv.76: 259-267.

Pressey, R. L., H. P. Possingham, and J. R. Day. 1997. Effectiveness of alternative heuristic algorithms for identifying indicative minimum requirements for conservation reserves. Biol. Conserv. 80: 207-219.

Pressey, R. L., C. J. Humphries, C. R. Margules, R. I. Vane-Wright, and P. H. Williams. 1993. Beyond opportunism: key principles for systematic reserve selection. Trend Ecol. Evol. 8: 124-128.

Pressey, R. L., S. Ferrier, T. C. Hager, C. A. Woods, S. L. Tully, and K. M. Weinman. 1996. How well protected are the forests of north-eastern New South Wales? - analyses of forest environments in relation to formal protection measures, land tenure, and vulnerability to clearing. Forest Ecology and Management. 85: 311-333.

Preston, F.W. 1960. Time and space and the variation of species. Ecology. 41: 611-627.

Preston, F.W. 1962. The canonical distribution of commonness and rarity. Ecology 43: 185-215.

Primmack, R. B. 1993. *Essentials of conservation biology*. Sinauer Associates Inc. Sunderland, USA.

Ramdass, I and M. Haniff. 1990. *A definition of priority conservation areas in Amazonia: Guyana country paper*. University of Georgetown. Georgetown, Guyana.

Rebelo, A.G. 1994. Using the Proteaceae to design a nature reserve network and determine priorities for the Cape Floristic Region. In: Forey, P.L., C.J. Humphries and R.I. Vane-Wright (eds.). *Systematics and conservation evaluation.* Clarendon. Oxford, UK. p. 375-396.

Rebelo, A.G. and W.R. Siegfried. 1990. Protection of the fynbos vegetation: ideal and real-world options. Biol. Conserv. 54: 15-31.

Reid, W. V. 1998. Biodiversity Hotspots. Trend. Ecol. Evol.13: 275-280.

Reyers, B., A.S. Van Jaarsveld, and M.A. McGeoch. 1998. National biodiversity risk assessment: a composite multivariate and index approach. Biodiversity and Conservation. 7: 945-965.

Richards, B.N., R.G. Bridges, R.A. Curtin, H.A. Nix, K.R. Sheperd and J. Turner. 1990. Biological conservation of the south-east forests: Report of the joint scientific committee. AGPS. Canberra, Australia.

Richardson, K.S. and V.A Funk. 1999. An approach to designing a protected area system in Guyana. Parks 9:7-16

Richerson, P.J. and K-L. Lunn. 1980. Patterns of plant species diversity in California: relation to weather and topography. Am. Nat. 116: 504-536.

Ricklefs, R.E. 1987. *Ecology*. Chiron. New York, USA.

Rosenzweig, M.L. and J. Winakur. 1969. Population ecology of desert rodent communities: habitats and environmental complexity. Ecology 50: 558-572.

Sampson, O.R and G.S. Bell. 1972. Vegetation types of Guyana: Photo interpretation key. Ministry of Mines and Forests of Guyana Forest Bulletin 4:59.

Schall, J,J. and E.R. Pianka. 1987. Geographical trend in the numbers of species. Science 201: 679-686.

Schnieder, C. and C. Moritz 1999. Rainforest refugia and evolution in Australia's Wet Tropics. Proc. R. Soc. Lond B. 266:191-196.

Schonewald-Cox , C.M. 1983. Guidelines to management: a beginning attempt. In: Schonewald-Cox, C.M., S.M. Chambers, B. MacBryde and W.L. Thomas (eds.) *Genetics and conservation: a reference for managing wild animal and plant populations.* The Benjamin/Cummings Publishing Company, Inc. Menlo Park, USA. p. 414-445.

Scott, J.M., B. Csuti, J.D. Jacobi, and J.E. Estes. 1987. Species richness: a geographic approach to protecting future biological diversity. Bioscience. 37: 782-788.

Scott, J.M., B. Csuti, K.Smith, J.E. Estes, and S. Caicco. 1988. Beyond endangered species: an integrated conservation strategy for the preservation of biological diversity. Endangered Species Update. 5:43-48.

Scott, J.M., F. Davis, B. Csuti, R. Noss, B. Butterfield, C. Groves, H. Anderson, S. Caicco, F. D'Erchia, T.C. Edwards, Jr., J. Ullimann, and R.G. Wright. 1993. A geographic approach to protection of biological diversity. Wildlife Monographs 57:1-41.

Shafer, C. L. 1990. *Nature Reserves: Island Theory and Conservation Practice.* Smithsonian Institution Press. Washington, USA.

Sisk, T.D., A.E. Launer, K.R. Switky and P.R. Ehrlich. 1994. Identifying extinction threats: global analyses of the distribution of biodiversity and the expansion of the human enterprise. Bioscience 44: 592-604.

Sizer, N. 1996. *Profit Without Plunder: Reaping Revenue From Guyana's Tropical Forests Without Destroying Them.* World Resources Institute. Washington, USA.

Snyder, D.B. 1966. *The birds of Guyana.* Peabody Museum. Cambridge, USA.

Soule, M. E. and M. A. Sanjayan 1998. Conservation Targets: Do they help? Science 279: 2060-2061.

Statistica 1999. STATISTICA for Windows. Statsoft inc. Tulsa, USA.

Stebbins, G.L. 1974. *Evolution Above Species Level.* Harvard University Press. Cambridge, USA.

Swanson, F.J and R.E. Sparks. 1990. Long-term ecological research and the invisible place. BioScience 40:502-508.

Stockwell, D. and D. Peters. 1999. The GARP modelling system: problems and solutions to automated spatial prediction. Int. J. GIS. 13: 143-158.

Stoms, D.M. 1992. Effects of habitat map generalization in biodiversity assessment. Photogrammetric Engineering and Remote Sensing. 58: 1587-1591.

Stoms, D.M. 1994. Scale dependence of species richness maps. Prof. Geog. 46: 346-358.

Terborgh, J. 1977. Bird species diversity on an Andean elevational gradient. Ecology 58: 1007-1019.

Terborgh, J. and B.Winters. 1983. A method for siting parks and reserves with special reference to Columbia and Ecuador. Biol. Conserv. 27: 45-58.

Ter Steege, H. 1998. The use of forest inventory data for a national protected area strategy in Guyana. Biodiversity and Conservation. 7: 1457-1483.

Thirgood, S. J. and M. F. Heath. 1994. Global patterns of endemism and the conservation of biodiversity. In: Forey, P.L., C.J. Humphries and R.I. Vane-Wright (eds.). *Systematics and conservation evaluation.* Clarendon. Oxford, UK. p. 207-227.

Tilman, D. 1982. *Resource Competition and Community Structure.* Princeton University Press. Princeton, USA.

Turner, M.G., R.H. Gardner, V.H. Dale, and R.V. O'Neil. 1989. Predicting the spread of disturbance across a heterogeneous landscape. Okios 55: 121-129.

Udvardy, M.F. 1975.A classification of the biogeographical provinces of the world. IUCN occasional paper, No.18. IUCN.Morges, Switzerland.

Underhill, L. G. 1994. Optimal and suboptimal reserve selection algorithms. Biol. Conserv.70: 85-87.

United Nations Development Program (UNDP). 1964. Soil map of Guyana. UNDP. New York, USA.

United States Overseas Aid (USAID). 1995. *Regionalization of Latin America and the Caribbean.* US Government publication. Washingtom, USA.

United States Geological Survey (USGS). 1996. Digital Elevation Model of South America. USGS EROS Data Center. Sioux Falls, USA.

University of Utrecht. 1995. Botanical Explorations in Guyana North & South Rupununi Savanna & Kanuku Mountains. University of Utrecht. Utrecht, Netherlands.

Usher, M.B. 1986. Wildlife conservation evaluation: attributes, criteria and values. Usher, M.B. (ed.). *Wildlife conservation evaluation*. Chapman and Hall. London, UK.

Van Jaarsveld, A. S., S. Freitag, S.L.Chown, C.Muller, S.Koch, H. Hull, C. Bellamy, M. Kruger, S.Endrody-Younga, M.W Mansell, and C.H. Scholtz. 1998. Biodiversity Assessment and Conservation Strategies. Science 279: 2106-2108.

Vane-Wright, R.I., C.J. Humphries, and P.H. Williams. 1991. What to protect ? Systematics and the agony of choice. Biol. Conserv. 55: 235-254.

Virolainen, K.M., T. Virola, J. Suhonen, M. Kuitunen, A. Lammi, and P. Siikamäki. 1999. Selecting networks of nature reserves: methods do affect the long-term outcome. Proc. R. Soc. Lond. B. 266: 1141-1146.

Walker, P. A. 1990. Modelling wildlife distributions using a geographic information system: kangaroos in relation to climate. J. Biogeog.17: 279-289.

Walker, P. A. and K. D. Cocks. 1991. Habitat: a procedure for modelling a disjoint environmental envelope for a plant or animal species. Global Ecology and Biogeography Letters 1: 108-118.

Walrond, W. 1987. Geology map of Guyana. Guyana Geology and Mining Commission. Georgetown, Guyana.

Wessels, K.J.,S. Freitag and A.S. Van Jaarsveld. 1999. The use of land facets as biodiversity surrogates during reserve selection at a local scale. Biol. Conserv. 89:21-38.

Whittaker, R.H. 1965. Dominance and diversity in land plant communities. Science 147: 250-260.

Whittaker, R.H. 1977. Evolution of species diversity in land communities. In: M. K.Hecht, W.C. Steere and B. Wallace (eds.) *Evolutionary Biology*. Plenum Press. New York, USA. p.1-67.

Wiens, J.A. 1989. Spatial scaling in ecology. Functional Ecology 3: 385-397

Williams, P.E. 1997. Land use and land degradation in Guyana. . In: Williams, P.E., J.T. Parry and M.J. Eden (eds.) *Land use, land degradation and land management in Guyana*. Commonwealth Geographical Bureau. Surrey, U.K. p. 1-18.

Williams, P.H.1993. Measuring more of biodiversity for choosing conservation areas, suing taxonomic relatedness. In: Moon, T-Y (ed.). *International*

Symposium on Biodiversity and Conservation. Korea University. Seoul, Korea. p.194-227.

Williams, P.H. and K.J.Gaston. 1994. Measuring more of biodiversity: can higher taxon richness predict wholesale species richness ? Biol. Conserv. 67: 211-217.

Williams, P. H. and C. J. Humphries. 1994. Biodiversity, taxonomic relatedness, and endemism in conservation. Systematics and Conservation Evaluation. 50: 69-287.

Williams, P., D. Gibbons, C. Margules, A. Rebelo, C. Humphries, and R. Pressey. 1996. A comparison of richness hotspots, rarity hotspots, and complementary areas for conserving diversity of British birds. Conserv. Biol. 10: 155-174.

Woodward, F.I. 1987. *Climate and Plant Distribution*. Cambridge University Press. Cambridge, UK.

World Bank. 1998. *Guyana: National Protected Areas System, Draft Proposal*. World Bank, Washington, USA.

World Conservation Monitoring Centre (WCMC). 1992. *Global Biodiversity: The Status of the Earth's Living Resources*. Chapman and Hall, London, UK.

World Conservation Union (IUCN). 1996. *1996 IUCN Red Data Book*. IUCN. Gland, Switzerland

Yee, T.W. and N.D. Mitchell. 1991. Generalised additive models in plant ecology. J. Veg. Science. 2: 587-602.

Appendix 1: Example of Database of Species Collections

INSTITUTS	COLLECTOR	COLL_NUM	FAMILY	GENUS	SPECIES
K	Maguire & Fanshawe	23312	CYPERACEAE	Rhynchospora	curvula
K	Jansen-Jacobs, M.J. et al	1838	CYPERACEAE	Rhynchospora	curvula
K,U	Sandwith, N.Y.	1445	CYPERACEAE	Rhynchospora	curvula
K	Jenman, G.S.	6124	CYPERACEAE	Rhynchospora	gigantea
K	Jenman, G.S.	6125	CYPERACEAE	Rhynchospora	gigantea
K	Jenman, G.S.	6123	CYPERACEAE	Rhynchospora	gigantea
K	Bacchus, Z. & R. Persaud	6	CYPERACEAE	Rhynchospora	gigantea
K	Bone, T. Maj.	343	CYPERACEAE	Rhynchospora	barbata
U	Maas, P.J.M. et al.	7265	CYPERACEAE	Bulbostylis	conifera
U, US	Stoffers, A.L. et al	181	CYPERACEAE	Bulbostylis	conifera
U	Dirven, Ir J.G.P.	LP187	CYPERACEAE	Bulbostylis	conifera
U	Maas, P.J.M. & Westra	3838	CYPERACEAE	Bulbostylis	conifera
U	Lindeman, J.C.	6677	CYPERACEAE	Bulbostylis	conifera
U	Cooper, A.	81	CYPERACEAE	Bulbostylis	conifera
U, US	Smith, A.C.	2198	CYPERACEAE	Bulbostylis	conifera
US	McDowell, T.	2514	CYPERACEAE	Bulbostylis	paradoxa
US	Gillespie, L.J.	2542	CYPERACEAE	Bulbostylis	paradoxa
US	Hahn, W.	5741	CYPERACEAE	Bulbostylis	paradoxa
US	Goodland, R.	701	CYPERACEAE	Bulbostylis	paradoxa
US	Gillespie, L.J.	1969	CYPERACEAE	Bulbostylis	capillaris
US	Hahn, W.	4418	CYPERACEAE	Bulbostylis	capillaris
US	Peterson, P.	7655	CYPERACEAE	Bulbostylis	conifera
US	Henkel, T.W.	2479	CYPERACEAE	Bulbostylis	conifera
US	Irwin, H.S.	319	CYPERACEAE	Bulbostylis	conifera
US	Goodland, R.	200	CYPERACEAE	Bulbostylis	conifera

K=Royal Botanic Garden at Kew, England; U= the University of Utrect Herbarium, the Netherlands; U=American Museum of Natural History, USA.

AUTHOR	COLLDATE	PROVINCE
Griseb.	8 May 1944	Potaro-Siparuni Region
Griseb.	26 September 1989	Upper Takutu-Upper Essequibo Region
Griseb.	9 September 1937	Potaro-Siparuni Region
Link	April 1889	Demerara-Mahaica Region
Link	April 1889	Demerara-Mahaica Region
Link	April 1889	Demerara-Mahaica Region
Link	21 July 1975	Pomeroon-Supenaam Region
(Vahl) Kunth	2 February 1931	Upper Takutu-Upper Essequibo Region
(Kunth) C.B. Clarke	4 sep 1988	Upper Takutu-Upper Essequibo Region
(Kunth) C.B. Clarke	5 Nov 1982	Upper Takutu-Upper Essequibo Region
(Kunth) C.B. Clarke	Feb-Mar 1952	Upper Takutu-Upper Essequibo Region
(Kunth) C.B. Clarke	20 October 1979	Upper Takutu-Upper Essequibo Region
(Kunth) C.B. Clarke	20 No? 1954	East Berbice-Corentyne Region
(Kunth) C.B. Clarke	Oct 1973	Mahaica-Berbice Region
(Kunth) C.B. Clarke	9-13 October 1937	Upper Takutu-Upper Essequibo Region
(Spreng.) Lindm.	26 April 1990	East Berbice-Corentyne Region
(Spreng.) Lindm.	29 October 1989	East Berbice-Corentyne Region
(Spreng.) Lindm.	17 March 1989	Potaro-Siparuni Region
(Spreng.) Lindm.	12 September 1963	Upper Takatu-Upper Essequibo Region
(L.) Clarke	3 July 1989	Upper Takatu-Upper Essequibo Region
(L.) Clarke	9 April 1988	Potaro-Siparuni Region
(Kunth) C.B. Clarke	1 July 1989	Upper Takutu-Upper Essequibo Region
(Kunth) C.B. Clarke	14 August 1993	East Berbice-Corentyne Region
(Kunth) C.B. Clarke	6 January 1955	East Berbice-Corentyne Region
(Kunth) C.B. Clarke	25-26 July 1963	Upper Takutu-Upper Essequibo Region

LOCALITY	ELEVM1	LAT_DGR	LAT_MIN	LONG_DGR	LONG_MIN
Kaieteur Plateau	300	05	10	059	29
Gunn's, Essequibo River	240	01	39	058	38
Kaieteur savanna	300	05	11	059	30
Lama Savanna		06	33	057	57
Lama Savanna		06	33	057	57
Lama Savanna		06	33	057	57
Mainstay Lake, Essequibo River	2	07	15	058	32
Annai savanna, Rupununi	46	03	57	059	06
Karanambo, near airstrip		03	45	058	19
Lethem (near), Rupununi		03	20	059	45
Rupununi		03	00	059	30
Rupununi distr, Manari		03	28	059	41
Corentyne River, Orealla savanna		05	19	057	20
Waramana, Berbice		05	35	060	44
Rupununi River basin, Karanambo		03	45	---	--
Orealla Amerindian village, Corentyn	20	05	20	057	22
Canje River, cow savanna, Digitima	10	05	33	057	40
Kato and vic.	750	04	40	059	55
Mountain View Hill, Rupununi savann	107	03	31	059	33
Towatawan Mts., 11 km E of Dadana	250	02	49	059	25
Mt. Kopinang, savanna at S base, alo	500	05	00	059	55
Shiriri Mt.	150	03	00	059	45
Takama Army Base, Berbice savann	100	05	43	057	57
Orealla savanna, Orealla Indian Reservation, Corenty		05	20	057	22
St. Ignatius, Rupununi	107	03	20	059	47

HABITAT
damp sand savanna
savanna
bare stoney ground

savanna, sandy clay with an overlay of lateitic gravel
on white clay savanna after long periods of drought
savanna
savanna
savanna
brown sand savana
open savana
white-tan sand savanna
sand savanna
at edge of forest
in savanna
granitic rock outcrop on hilltop
im moist depressions
open savanna
in savanna
in savanna
in savanna, grassland