

**THE INVERTEBRATES OF INDIGENOUS FORESTS IN LIMPOPO PROVINCE,
SOUTH AFRICA: DIVERSITY, BIOGEOGRAPHY AND CONSERVATION**

by

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ABSTRACT

In this study I investigated patterns of invertebrate diversity in Limpopo Province indigenous forests, in order to highlight forests and taxa of special conservation significance. Invertebrates from seven target taxa were sampled in 11 patches of indigenous forest in Limpopo Province from February 2001 to January 2002, including six forests in the Soutpansberg and five forests in the northern Drakensberg. Selected forests comprise three distinct vegetation subtypes and the target taxa selected were millipedes, centipedes, earthworms, terrestrial molluscs, spiders, scorpions and amphipods. Invertebrates were sampled by active searching of quadrats and line transects and pitfall traps. A total of 11 969 indigenous target group individuals were sampled, comprising 14 orders, 50 families, 86 genera and 142 species (including at least nine new).

There was a significant difference in the total invertebrate species richness and diversity of forest patches but results varied considerably when different target group figures were analyzed. With the exception of spiders, the factors influencing total and individual target group richness in forests could not be determined. Introduced invertebrates comprised a large proportion of the species and individuals sampled, but were not shown to affect indigenous fauna.

Invertebrate species assemblages were most similar between forests sharing the same vegetation subtype and between forests in the same mountain region. However, each forest patch had unique species and some even had unique families. Limpopo Province forests support high numbers of endemic invertebrates. A total of 47 endemic invertebrate species were sampled, including six site endemics, eight local endemics, nine regional endemics and 24 national endemics. The numbers and scales of endemism varied by target group. Invertebrate species' distributions in Limpopo Province forests generally support the biogeographic theories of Pleistocene forest refugia and the Limpopo River valley as a radiation barrier, although some important contradictions were found. Local endemism in Limpopo Province forests is likely the product of historical processes.

Although some significant relationships were found between surrogate and true measures, single taxon biodiversity indicators, the higher taxon method, morphospecies and land classes could not accurately predict patterns of target invertebrate species richness in

Limpopo Province forests. Results show that formal species identification should be used if accurate richness estimates are desired; the use of surrogates is not supported by this study.

Conservation of Limpopo Province forests is vital for the preservation of valuable invertebrate communities. No forest sampled in this study can be considered unimportant. Effective forest conservation and management is dependent upon the protection of forests of varying patch size, careful evaluation and control of utilization and the establishment and maintenance of corridors linking isolated forest patches.

PREFACE

The experimental work described in this dissertation was carried out in the School of Botany and Zoology, University of KwaZulu-Natal, Pietermaritzburg, from January 2000 to December 2003, under the supervision of Dr Michelle Hamer and co-supervision of Professor Michael Lawes.

These studies represent original work by the author and have not otherwise been submitted in any form for any degree or diploma to any University. Where use has been made of the work of others it is duly acknowledged in the text.

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TABLE OF CONTENTS

	Page
ABSTRACT	ii
PREFACE	iv
TABLE OF CONTENTS	v
LIST OF TABLES	ix
LIST OF FIGURES	xiii
ACKNOWLEDGEMENTS	xviii
CHAPTER 1: GENERAL INTRODUCTION	1
1.1 BIODIVERSITY	1
1.1.1 What is biodiversity?	1
1.1.2 The three levels of biodiversity	3
1.1.3 Estimating global species diversity	4
1.1.4 Invertebrate abundance and diversity	5
1.1.5 Benefits of biodiversity to humans	7
1.1.6 Global species extinction	9
1.1.7 Threats to global biodiversity	10
1.2 FOREST BIODIVERSITY	13
1.2.1 Global forests and biodiversity	13
1.2.2 Forest invertebrate abundance and diversity	14
1.2.3 Why study forest invertebrates?	16
1.3 SOUTH AFRICAN FORESTS	18
1.3.1 Description of South African forests	18
1.3.2 South African forest classification	21
1.3.3 South African Afromontane forests	22
1.4 PURPOSE AND OBJECTIVES	24
CHAPTER 2: STUDY SITES, TAXA AND METHODS	27
2.1 INTRODUCTION	27
2.1.1 Northern Mistbelt Forests of Limpopo Province	27
2.1.2 Species vs. morphospecies in biodiversity studies	29
2.1.3 Focal groups vs. target groups	31
2.1.4 Invertebrate collection techniques	32
2.2 STUDY SITES	34
2.3 STUDY TAXA	38
2.3.1 Millipedes (Class: Diplopoda)	38
2.3.2 Centipedes (Class: Chilopoda)	40
2.3.3 Scorpions (Order: Scorpionida)	41
2.3.4 Web building and ground wandering spiders (Order: Araneae)	42
2.3.5 Terrestrial molluscs (Class: Gastropoda)	44
2.3.6 Earthworms (Class: Oligochaeta)	46
2.3.7 Terrestrial amphipods (Family: Talitridae)	47
2.3.8 Additional taxa	48
2.4 METHODS	48

2.4.1	Quadrat sampling	48
2.4.2	Line transect sampling	50
2.4.3	Pitfall trap sampling	51
2.4.4	Other sampling techniques	52
2.4.5	Specimen identification	53
CHAPTER 3: INVERTEBRATE SPECIES DIVERSITY OF LIMPOPO PROVINCE FORESTS		
	PROVINCE FORESTS	55
3.1	INTRODUCTION	55
3.1.1	Biodiversity surrogates	55
3.1.2	Measuring alpha diversity	56
3.1.3	Introduced species	59
3.2	METHODS	60
3.2.1	Calculations of richness, diversity and evenness	61
3.2.2	Comparisons of richness, diversity and evenness	61
3.2.3	Absolute species richness, diversity and evenness	61
3.2.4	Descriptive models - multiple regression analysis	62
3.2.5	Introduced species	63
3.3	RESULTS	63
3.3.1	Total numbers of species and individuals	63
3.3.2	Regional comparisons of richness, diversity and evenness	67
3.3.3	Comparisons of forest richness, diversity and evenness	67
3.3.4	Comparisons of target group richness, diversity and evenness	71
3.3.5	Absolute species richness, diversity and evenness	75
3.3.6	Descriptive models - multiple regression analysis	75
3.3.7	Introduced species	77
3.4	DISCUSSION	80
3.4.1	Species composition	80
3.4.2	Regional richness, diversity and evenness	81
3.4.3	Forest richness, diversity and evenness	82
3.4.4	Target group richness, diversity and evenness	83
3.4.5	Introduced species	89
3.5	CONCLUSION	91
CHAPTER 4: INVERTEBRATE COMMUNITIES, DISTRIBUTION AND BIOGEOGRAPHY		
	BIOGEOGRAPHY	93
4.1	INTRODUCTION	93
4.1.1	Measuring beta diversity	94
4.1.2	Species endemism	95
4.1.3	Limpopo Province forest history in brief	96
4.2	METHODS	98
4.2.1	Site similarity	98
4.2.2	Cluster analysis	98
4.2.3	Species endemism analysis	99

4.2.4 Comparison with Zimbabwean and KwaZulu-Natal forests	101
4.3 RESULTS	103
4.3.1 Site similarity	103
4.3.2 Cluster analysis	109
4.3.3 Species endemism analysis	109
4.3.4 Comparison with Zimbabwean and KwaZulu-Natal forests	123
4.4 DISCUSSION	127
4.4.1 Site similarity	127
4.4.2 Endemism	128
4.4.3 Forest history and invertebrate distribution	133
4.5 CONCLUSION	135
CHAPTER 5: ASSESSMENT OF BIODIVERSITY SURROGATES	137
5.1 INTRODUCTION	137
5.1.1 Biodiversity indicators and invertebrate studies	139
5.1.2 Land classes as surrogates for species' distributions	143
5.2 METHODS	145
5.2.1 Individual taxa as indicators of species richness	146
5.2.2 Higher taxa as indicators of invertebrate species richness	146
5.2.3 Morphospecies as indicators of formal (true) invertebrate species richness	147
5.2.4 Vegetation classification as a surrogate for invertebrate species' distributions	148
5.3 RESULTS	148
5.3.1 Individual taxa as indicators of species richness	148
5.3.2 Higher taxa as indicators of invertebrate species richness	154
5.3.3 Morphospecies as indicators of formal (true) invertebrate species richness	159
5.3.4 Vegetation classification as a surrogate for invertebrate species' distributions	165
5.4 DISCUSSION	165
5.4.1 Individual taxa as indicators of species richness	165
5.4.2 Higher taxa as indicators of invertebrate species richness	169
5.4.3 Morphospecies as indicators of invertebrate species richness	171
5.4.4 Vegetation classification as a surrogate for invertebrate species' distributions	173
5.5 CONCLUSION	175
CHAPTER 6: SUMMARY AND CONSERVATION RECOMMENDATIONS	176
6.1 INTRODUCTION	176
6.1.1 Uses of and threats to South African forests	176
6.1.2 South African forest conservation	178
6.1.3 Limpopo Province forest conservation at present	180

6.2 LIMPOPO PROVINCE FOREST INVERTEBRATES	181
6.2.1 Invertebrate species diversity - major findings	181
6.2.2 Invertebrate communities, distribution and biogeography- major findings	182
6.2.3 Assessment of biodiversity surrogates - major findings	183
6.2.4 Additional information	184
6.3 CONSERVATION OF LIMPOPO PROVINCE FORESTS	188
6.3.1 Why conserve Limpopo Province forests?	188
6.3.2 Which forests should be conserved in Limpopo Province?	188
6.3.3 How should we conserve forests in Limpopo Province?	191
6.4 CONCLUSION	192
REFERENCES	194
APPENDICES	222

LIST OF TABLES

	Page
Table 1.1: Afromontane forest by province in South Africa. The total area of the Afromontane forest in each province, the proportion of the province area that Afromontane vegetation occupies and the contribution to the total area of Afromontane forest in South Africa are given (Low & Rebelo 1996).	23
Table 2.1: Characteristics of forest patches sampled in this study. The name, location, size, forest subtype and vegetation characteristics of each forest are given (Geldenhuys & Venter 2002; von Maltitz <i>et al.</i> 2003), with species percents calculated.	35
Table 3.1: Biotic and abiotic variables assessed in the multiple regression analysis.	62
Table 3.2: Total numbers of indigenous target group families, genera, species and (individuals) sampled in Limpopo Province forests. Forest names are abbreviated as follows: Hanglip = HAN, Roodewal = ROD, Goedehoop = GHP, Ratombo = RAT, Entabeni = ENT, Thathe Vondo = TV, Grootbosch = GRO, New Agatha = NAG, Swartbos = SWB, Baccarat = BAC, Forest Glens = FGL. Taxa that could not be identified beyond order are indicated by (*).	64
Table 3.3: Percentage of the total number of recognized South African (SA) species and families represented in this study. Introduced species, new species and species that could not be identified are excluded.	65
Table 3.4: Significant differences in richness (▲) and diversity (■) between forests, where $P < 0.05$ (post hoc test LSD). Shaded symbols indicate that the forest in the left column was higher and unshaded symbols indicate that the forest in the top row was higher. Forest names are abbreviated as follows: Hanglip = HAN, Roodewal = ROD, Goedehoop = GHP, Ratombo = RAT, Entabeni = ENT, Thathe Vondo = TV, Grootbosch = GRO, New Agatha = NAG, Swartbos = SWB, Baccarat = BAC, Forest Glens = FGL.	70
Table 3.5: Significant differences in richness (▲), diversity (■) and evenness (●) between forests for a) millipedes, b) molluscs and c) web building spiders, where $P < 0.05$ (post hoc test LSD). Shaded symbols indicate that the forest in the left column was higher and unshaded symbols indicate that the forest in the top row was higher. Forest names are abbreviated as follows: Hanglip = HAN, Roodewal = ROD, Goedehoop = GHP, Ratombo = RAT, Entabeni = ENT, Thathe Vondo = TV, Grootbosch = GRO, New Agatha = NAG, Swartbos = SWB, Baccarat = BAC, Forest Glens = FGL.	74
Table 3.6: Absolute species richness (RI_{ab} , $R2_{ab}$ and S_{ab}), diversity (NI_{ab}) and evenness ($E5_{ab}$) for the two sampled regions.	75

	Page
Table 3.7: Absolute species richness (S_{ab}), diversity (NI_{ab}) and evenness ($E5_{ab}$) for each sampled forest and major target group. Spider calculations include both web building and ground wandering spiders. Forest names are abbreviated as follows: Hanglip = HAN, Roodewal = ROD, Goedehoop = GHP, Ratombo = RAT, Entabeni = ENT, Thathe Vondo = TV, Grootbosch = GRO, New Agatha = NAG, Swartbos = SWB, Baccarat = BAC, Forest Glens = FGL.	76
Table 3.8: Comparative millipede richness values for relatively well-sampled forest sites in South Africa (National Millipede Database).	85
Table 4.1: Similarities in invertebrate family and species composition between Limpopo Province forests. Jaccard similarity coefficients are given for forests sharing a) 30% or more of their invertebrate species and b) 55% or more of their invertebrate families. All values have been multiplied by 100 for ease of interpretation. Forest names are abbreviated as follows: Hanglip = HAN, Roodewal = ROD, Goedehoop = GHP, Ratombo = RAT, Entabeni = ENT, Thathe Vondo = TV, Grootbosch = GRO, New Agatha = NAG, Swartbos = SWB, Baccarat = BAC, Forest Glens = FGL. The bold lines encircle forests located in the same region. Forests sharing the mistbelt forest subtype are indicated by shading.	105
Table 4.2: Significant differences in numbers of endemic species between forests when all endemics (●) and Limpopo Province forest endemics (■) are considered, where $P < 0.05$ (post hoc test LSD). Shaded symbols indicate that the forest in the left column was higher and unshaded symbols indicate that the forest in the top row was higher. Forest names are abbreviated as follows: Hanglip = HAN, Roodewal = ROD, Goedehoop = GHP, Ratombo = RAT, Entabeni = ENT, Thathe Vondo = TV, Grootbosch = GRO, New Agatha = NAG, Swartbos = SWB, Baccarat = BAC, Forest Glens = FGL.	119
Table 4.3: Similarities in millipede genus composition between regional forests (Jaccard similarity coefficients). All values have been multiplied by 100 for ease of interpretation. The following abbreviations have been used: Zimbabwe = eastern highlands of Zimbabwe, KZN = KwaZulu-Natal and LP = Limpopo Province.	124
Table 4.4: Similarities in mollusc a) species and b) genera composition between regional forests (Jaccard similarity coefficients). All values have been multiplied by 100 for ease of interpretation. The following abbreviations have been used: Zimbabwe = eastern highlands of Zimbabwe, KZN = KwaZulu-Natal and LP = Limpopo Province.	126
Table 4.5: The numbers of site and national endemic millipedes in selected South African forested sites (from Hamer & Slotow 2002). Forests are listed in descending order of total millipede endemics. Because of differences between definitions, the local and regional levels could not be compared, but these numbers are included as national endemics.	131
Table 5.1: Some suggested invertebrate bioindicators	138

	Page
Table 5.2: Summary of the relationships between total target invertebrate species richness (total <i>S</i>) and the richness (<i>S</i>) of each taxon investigated. Note that there were no significant relationships.	149
Table 5.3: Relationship matrix for species richness (<i>S</i>) of invertebrates, plants and birds in Limpopo Province forests (R = linear regression results, C = Pearson's correlation coefficient). The only significant relationship was between millipede and centipede richness.	152
Table 5.4: Relationship matrix for species, genus and family richness (<i>S</i>) of target group invertebrates in Limpopo Province forests (R = linear regression results, C = Pearson's correlation coefficient).	154
Table 5.5: Ranking of forests for hypothetical conservation prioritization, in order of decreasing richness at three taxonomic levels. Parentheses indicate the richness (<i>S</i>) of forests at each taxonomic level.	159
Table 5.6: Summary of the relationships between the morphospecies richness (<i>S</i>) and true species richness (<i>S</i>) of each group investigated. Note that all relationships were significant ($P < 0.01$).	163
Table 5.7: Summary of significant correlations in taxon richness across sites in various habitats (Significant correlations: $P < 0.05$), listed in order of decreasing proportion of significant positive correlations. Only recent (1996+) studies that have included invertebrate taxa are listed.	167
Table 5.8: Sampling frequency, richness and morphospecies error for invertebrate groups. 'Other' taxa are those that were not considered for the morphospecies analysis and include amphipods, scorpions, butterflies, dragonflies, flies and non-target invertebrates sampled in pitfall traps.	172
Table 6.1: Area and proportion of different forest types conserved in southern Africa (Low & Rebelo 1996).	179
Table 6.2: Management classifications of Limpopo Province forests protected by DWAF (DWAF unpublished reports a & b).	181
Table 6.3: 'Special species' sampled in Limpopo Province forests. New species, potentially new species and target group endemics are not included. The categories are defined as follows: Important record = the sampled locality is new and contributes to the species' distribution. Northernmost record = species' presences in the study area was previously known and is the northernmost extent of the species' distribution. Endemic = non-target group species or subspecies that is endemic. Rare = species rare in South Africa. The following abbreviations are used: SPB = Soutpansberg, DKB = Drakensberg, LP = Limpopo Province, KZN = KwaZulu-Natal, GP = Gauteng Province, MP = Mpumalanga Province, SA = South Africa.	187

	Page
Table 6.4: Differential ranking of forests for conservation based on six individual criteria. Forests are listed in descending order. Only indigenous target group invertebrate species were considered. Values for each category are indicated by parentheses.	190

LIST OF FIGURES

	Page
Figure 1.1: Altitudinal distribution of South African forests (from von Maltitz <i>et al.</i> 2003). The area covered in this study is demarcated in blue.	19
Figure 2.1: Distribution of forests studied in Limpopo Province and associated forest subtypes (modified from Geldenhuys & Venter 2002). Outlined regions are conservation areas and nature reserves managed by the Department of Water Affairs and Forestry. Study sites are indicated by shading.	36
Figure 2.2: Standard quadrat size and shape for active sampling of ground-dwelling invertebrates.	49
Figure 3.1: Sampling frequency of target groups in Limpopo Province forests, expressed as the percentage of the total number of indigenous target group individuals sampled (parentheses indicate the number of individuals sampled).	66
Figure 3.2: Distribution of indigenous species among the target groups in Limpopo Province forests, expressed as the proportion of the total number of species in each target group (parentheses indicate the number of species).	66
Figure 3.3: Target group a) richness S , b) diversity NI and c) evenness $E5$ of the Soutpansberg and Drakensberg regions and 95% confidence limits.	68
Figure 3.4: Target group a) richness S , b) diversity NI and c) evenness $E5$ for each of the 11 forests sampled and 95% confidence limits. Forest names are abbreviated as follows: Hanglip = HAN, Roodewal = ROD, Goedeheop = GHP, Ratombo = RAT, Entabeni = ENT, Thathe Vondo = TV, Grootbosch = GRO, New Agatha = NAG, Swartbos = SWB, Baccarat = BAC, Forest Glens = FGL.	69
Figure 3.5: Richness (S) of a) millipedes, b) centipedes, c) earthworms and d) molluscs in each forest sampled and 95% confidence limits. Forest names are abbreviated as follows: Hanglip = HAN, Roodewal = ROD, Goedeheop = GHP, Ratombo = RAT, Entabeni = ENT, Thathe Vondo = TV, Grootbosch = GRO, New Agatha = NAG, Swartbos = SWB, Baccarat = BAC, Forest Glens = FGL.	72
Figure 3.6: Richness (S) of a) web building spiders, b) ground wandering spiders and c) amphipods in each forest sampled and 95% confidence limits. Forests lacking symbols indicates absences. Forest names are abbreviated as follows: Hanglip = HAN, Roodewal = ROD, Goedeheop = GHP, Ratombo = RAT, Entabeni = ENT, Thathe Vondo = TV, Grootbosch = GRO, New Agatha = NAG, Swartbos = SWB, Baccarat = BAC, Forest Glens = FGL.	73
Figure 3.7: The number of introduced earthworm and mollusc species recorded in each forest. Forest names are abbreviated as follows: Hanglip = HAN, Roodewal = ROD, Goedeheop = GHP, Ratombo = RAT, Entabeni = ENT, Thathe Vondo = TV, Grootbosch = GRO, New Agatha = NAG, Swartbos = SWB, Baccarat = BAC, Forest Glens = FGL.	78

	Page
Figure 3.8: The proportion of introduced earthworms in forests for a) the total number of earthworm species and b) the total number of earthworm individuals. Forest names are abbreviated as follows: Hanglip = HAN, Roodewal = ROD, Goedehoop = GHP, Ratombo = RAT, Entabeni = ENT, Thathe Vondo = TV, Grootbosch = GRO, New Agatha = NAG, Swartbos = SWB, Baccarat = BAC, Forest Glens = FGL.	78
Figure 3.9: The numbers of indigenous and introduced earthworm species in Limpopo Province forests and 95% confidence limits.	79
Figure 4.1: The contribution of the three Limpopo Province forest subtypes to invertebrate richness where a) is the species composition and b) is the family composition. The mistbelt forest subtype has been divided according to region.	106
Figure 4.2: The contribution of each forest sampled in Limpopo Province to invertebrate diversity where a) is the species composition and b) is the family composition. Forest names are abbreviated as follows: Hanglip = HAN, Roodewal = ROD, Goedehoop = GHP, Ratombo = RAT, Entabeni = ENT, Thathe Vondo = TV, Grootbosch = GRO, New Agatha = NAG, Swartbos = SWB, Baccarat = BAC, Forest Glens = FGL. Forest names are coded by vegetation subtype (M = mistbelt forest, SS = semi-deciduous scrub forest, SM = semi-deciduous mixed forest).	107
Figure 4.3: Comparison of the invertebrate composition of forest regions with individual forests. Jaccard similarity coefficients for the number of species and (families) shared between a) all Soutpansberg forests and each forest sampled in the Drakensberg and b) all Drakensberg forests and each forest sampled in the Soutpansberg. All values have been multiplied by 100 for ease of interpretation. Dotted lines indicate where map areas have been removed. See Figure 2.1 (pg. 36) for actual distances between regions.	108
Figure 4.4: Dendrograms for a) all target invertebrate species, b) millipede species and c) centipede species shared between forests using the average linkage between forests and Euclidean distances. Forest names are abbreviated as follows: Hanglip = HAN, Roodewal = ROD, Goedehoop = GHP, Ratombo = RAT, Entabeni = ENT, Thathe Vondo = TV, Grootbosch = GRO, New Agatha = NAG, Swartbos = SWB, Baccarat = BAC, Forest Glens = FGL. Forests are coded by vegetation subtype (1 = mistbelt forest, 2 = semi-deciduous mixed forest, 3 = semi-deciduous scrub forest) and region (S = Soutpansberg, D = Drakensberg).	110
Figure 4.5: Dendrograms for a) mollusc, b) earthworm and c) spider species shared between forests using the average linkage between forests and Euclidean distances. Forest names are abbreviated as follows: Hanglip = HAN, Roodewal = ROD, Goedehoop = GHP, Ratombo = RAT, Entabeni = ENT, Thathe Vondo = TV, Grootbosch = GRO, New Agatha = NAG, Swartbos = SWB, Baccarat = BAC, Forest Glens = FGL. Forests are coded by vegetation subtype (1 = mistbelt forest, 2 = semi-deciduous mixed forest, 3 = semi-deciduous scrub forest) and region (S = Soutpansberg, D = Drakensberg).	111

	Page
Figure 4.6: Levels of endemism in six target taxa in all Limpopo Province forests sampled, excluding introduced species and those species that could not be identified. Figures above each bar indicate the total number of indigenous species identified in each taxon.	112
Figure 4.7: The number of endemics and 95% confidence limits for each region sampled, with the total number of endemics (all levels, ●) and Limpopo Province forest endemics (regional, local and site levels, □). 114	
Figure 4.8: The number of endemics and 95% confidence limits for each forest subtype sampled, with the total number of endemics (all levels, ●) and Limpopo Province forest endemics (regional, local and site levels, □). 114	
Figure 4.9: Taxon contributions to the total number of endemic species recorded in each forest. Numbers include site, local, regional and national endemics. Forest names are abbreviated as follows: Hanglip = HAN, Roodewal = ROD, Goedehoop = GHP, Ratombo = RAT, Entabeni = ENT, Thathe Vondo = TV, Grootbosch = GRO, New Agatha = NAG, Swartbos = SWB, Baccarat = BAC, Forest Glens = FGL.	116
Figure 4.10: The numbers and levels of endemic species (for all target taxa) sampled in each forest, excluding introduced species and those species that could not be identified. Forest names are abbreviated as follows: Hanglip = HAN, Roodewal = ROD, Goedehoop = GHP, Ratombo = RAT, Entabeni = ENT, Thathe Vondo = TV, Grootbosch = GRO, New Agatha = NAG, Swartbos = SWB, Baccarat = BAC, Forest Glens = FGL.	117
Figure 4.11: The number of endemics for each sampled forest, with the total endemics (all levels, ●), Limpopo Province forest endemics (regional, local and site levels, □) and 95% confidence limits. Forest names are abbreviated as follows: Hanglip = HAN, Roodewal = ROD, Goedehoop = GHP, Ratombo = RAT, Entabeni = ENT, Thathe Vondo = TV, Grootbosch = GRO, New Agatha = NAG, Swartbos = SWB, Baccarat = BAC, Forest Glens = FGL.	118
Figure 4.12: The relationship between species richness (<i>S</i>) and the number of local endemic species in Limpopo Province forests, with Roodewal and Ratombo included (dotted line) and without Roodewal and Ratombo (solid line). Forest names are abbreviated as follows: Hanglip = HAN, Roodewal = ROD, Goedehoop = GHP, Ratombo = RAT, Entabeni = ENT, Thathe Vondo = TV, Grootbosch = GRO, New Agatha = NAG, Swartbos = SWB, Baccarat = BAC, Forest Glens = FGL.	121
Figure 4.13: The relationship between the distance from site of forest refuge (connectivity to regional species pool) and the number of local endemics in Limpopo Province forests, when a) Ngome Forest and b) Mariepskop Forest are used as forest refuge sites. Note that both relationships were significant.	122

	Page
Figure 4.14: Dendrogram for millipede genera shared between regional forests using the average linkage between groups and Euclidean distances. The following abbreviations have been used: Zimbabwe = eastern highlands of Zimbabwe, KZN = KwaZulu-Natal and LP = Limpopo Province.	124
Figure 4.15: Dendrograms for mollusc a) species and b) genera shared between regional forests using the average linkage between groups and Euclidean distances. The following abbreviations have been used: Zimbabwe = eastern highlands of Zimbabwe, KZN = KwaZulu-Natal and LP = Limpopo Province.	126
Figure 4.16: Two possible orientations of dispersal corridors between Drakensberg and Soutpansberg forests in Limpopo Province. The solid line indicates the orientation supported by the results of the present study. The dotted line indicates the shortest possible corridor.	128
Figure 5.1: The use of individual invertebrate taxa as indicators of the species richness of all indigenous target invertebrates. Note that none of these relationships were significant.	150
Figure 5.2: The use of individual non-invertebrate taxa as indicators of the species richness of all indigenous target invertebrates. Note that neither relationship was significant.	151
Figure 5.3: The use of centipedes as indicators of millipede species richness. The relationship between centipede and millipede species richness was significant.	153
Figure 5.4: Distribution of indigenous species among families and genera in all Limpopo Province forests for a) millipedes and b) centipedes. The number of species in each genus is indicated in parentheses. The Geophilomorpha have been excluded from the centipede graph since they could not be identified beyond order level.	155
Figure 5.5: Distribution of indigenous species among families and genera in all Limpopo Province forests for a) earthworms and b) molluscs. The number of species in each genus is indicated in parentheses. ‘Other families’ of molluscs include Achatinidae, Chlamydephoridae, Clausiliidae, Euconulidae, Helicarionidae and Pomatisidae, each with one genus and one species.	156
Figure 5.6: Distribution of indigenous spider species among families and genera in all Limpopo Province forests. The number of species in each genus is indicated in parentheses. Only genera with two or more species are named. ‘Other families’ of spiders include Anapidae, Clubionidae, Corinnidae, Ctenidae, Cyatholipidae, Dipluridae, Hahniidae, Mimetidae, Nesticidae, Orsolobidae, Phyxelididae and Zodariidae, each with one genus and one species.	157

	Page
Figure 5.7: The use of higher taxa as surrogates of species richness, comparing the genus (\times) and family (Δ) levels to species. The values represent the 11 forests sampled. The genera are better surrogates because they more closely approximate the 45° angle (dotted line).	158
Figure 5.8: The total true invertebrate species richness (S) and morphospecies richness (S) of target groups and 95% confidence limits. The numbers include all indigenous and exotic target invertebrates and ants sampled by all methods, including randomly collected individuals.	160
Figure 5.9: The true species richness (S , Δ) and morphospecies richness (S , \times) of each invertebrate taxon and 95% confidence limits. The numbers include all indigenous and exotic invertebrates sampled with all methods, including randomly collected individuals.	161
Figure 5.10: The use of morphospecies as surrogates of species richness for each invertebrate group. Centipede morphospecies most accurately reflect true species because this line most closely approximates the 45° angle. Earthworm morphospecies numbers were the least accurate.	162
Figure 5.11: The relative amount of splitting and lumping of true species when using morphospecies. ‘All groups’ includes the taxa shown, amphipods and scorpions.	164
Figure 6.1: The proportion (and number) of Red Listed invertebrate species, including terrestrial, marine and freshwater species, as a percentage of all South African animal species listed (IUCN 2002).	186

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CHAPTER 1

GENERAL INTRODUCTION

1.1 BIODIVERSITY

1.1.1 What is biodiversity?

The term and concept of biodiversity, a jargon contraction for biological or biotic diversity, did not officially exist twenty years ago (Wilson 1997) and there was little expressed interest in the idea (Younes 1996). The word ‘biodiversity’ was first used publicly only in 1986 during the National Forum on BioDiversity held in Washington, D.C. and since then the term has become a part of popular language and is one of the most frequently used expressions in the biological sciences today (Spellerberg 1996c; Wilson 1997).

‘Biodiversity’ could be defined simply as ‘the diversity of life,’ but this definition does not emphasize the complete meaning or complexity of the term. During the XVII General Assembly of the International Union for the Conservation of Nature and Natural Resources (Costa Rica, February 1988), the Species Survival Commission adopted the following definition of ‘biodiversity:’

The variety and variability of all living organisms. This includes the genetic variability within species and their populations, the variety of species and their life forms, the diversity of the complexes of associated species and of their interactions, and of the ecological processes that they influence or perform (Huntley 1989).

E. O. Wilson (1997), who has done much to promote the concept, defines ‘biodiversity’ as follows:

All hereditarily based variation at all levels of organization, from the genes within a single local population or species, to the species composing all or part of a local community, and finally to the communities themselves that compose the living parts of the multifarious ecosystems of the world.

Generally, ‘biodiversity’ is an attempt to describe the complexity of life on Earth, to further our understanding of it and to promote its maintenance (Gaston & Spicer 1998).

Although it is a term commonly used and is generally recognized as being important, biodiversity is defined in many ways by many people (Stork 1993; Patrick 1997; Burley 2002), perhaps indicating its complex and multifaceted nature (Heywood & Baste 1995). According to Heywood and Baste (1995), people living in developed countries understand biodiversity differently from those in developing countries, as do those living in cities versus rural areas. Even individual scientists and special interest groups perceive biodiversity in various ways, giving rise to more than 12 formal published definitions of the term (Gaston & Spicer 1998). As a result, the concept is confusing to many people and is sometimes incorrectly equated simply with nature, wildlife or single species and its conservation thought to involve only rare or endangered species or communities (Spellerberg 1996c; Hunter 1999). These differing and sometimes incorrect and incomplete perceptions of biodiversity have often caused conflict and confusion in policy, in science, and among the public (Burley 2002).

It is important to recognize that the concept of biodiversity is not simply concerned with species, but includes the variation in the genetics within a single species and variation through families, genera, populations, communities, habitats and even ecosystems (Wilson 1992). It also includes the microbes, fungi and invertebrates that are so often overlooked (Hunter 1999). Recently the human dimension has also been added to the scope of biodiversity, since we need to understand the cycles of interactions between biodiversity and human populations in order to effectively direct conservation and sustainable use measures (Heywood & Baste 1995).

Conservation of biodiversity is not simply protecting a popular mammal species or colourful flower, but is the conservation of all variety, interactions between species, ecosystem and evolutionary processes, rare subspecies and many other important aspects of biodiversity in the context of human cultures (Heywood & Baste 1995; Spellerberg 1996c; Hunter 1999). It is also protecting genetic variation and sources of food, materials and medicines (Spellerberg 1996a). Wise management policy and decision-making at national and international levels are only possible with such a complete understanding of biodiversity (Spellerberg 1996c).

1.1.2 The three levels of biodiversity

In an attempt to simplify its complexities, biologists usually describe, quantify and manage biodiversity at three distinct levels: genetic diversity, species diversity and ecosystem diversity (Stork 1993; Barbier *et al.* 1994; Burley 2002). Although they are often viewed as separate disciplines, all three levels are interlinked and interdependent (Heywood & Baste 1995) and are part of a continuum including populations, communities, habitats, niches, landscapes, continents and historical levels (Holloway & Stork 1991).

Genetic diversity, or intraspecific diversity, is the variation of heritable genetic material among species, among populations, among individuals within a population and within individuals (Hunter 1999; Dajoz 2000; Burley 2002). Genetic diversity is usually measured by differences between genes, DNA or amino acid sequences, breeds, strains and distinct populations (Heywood & Baste 1995). The measurement and interpretation of this level of diversity is problematic, since molecular genetic analysis may not correspond to major morphological differences and the exploration of genetics usually requires certain expertise and the skills of geneticists (Bond 1989a; Spellerberg 1996a). However, genetic diversity is the foundation of all evolutionary processes and all other levels of biodiversity (Spellerberg 1996a) and is valuable in studying population structure, inbreeding and gene flow. Genetic diversity is of particular interest to geneticists, breeders and phylogeographers (Burley 2002).

Species diversity describes the number, abundance or rarity and endemism of species (Burley 2002) and the interactions between species in a community (Spellerberg 1996a). Common measures of species diversity include species richness, or the number of species, species composition, or the species assemblage, and species diversity, or the relative abundance of the species in an area (Spellerberg 1996c). Each natural community has a unique, characteristic species biodiversity, in terms of both the number and composition of species (Lovejoy 1997). Species diversity is of special concern to taxonomists, ecologists and conservationists (Bond 1989a; Burley 2002).

Ecosystem or ecological diversity is the variation of ecosystems in landscapes and biomes, including the way in which populations of species interact with each other and their environment, the ecological roles of species, the global and local composition, structure

and function of ecosystems, the processes and interactions between ecosystems and the existence of biodiversity ‘hotspots’ (Heywood & Baste 1995; Burley 2002). Although ecosystems can be difficult to define, there are evident patterns of organism distribution and this level is a method of organizing the understanding of such patterns (Hunter 1999). Ecosystem diversity is measured at a global scale in terms of biogeographical units, sub-components and processes (Spellerberg 1996a) and is of interest to ecologists and ecosystem/landscape managers (Burley 2002). This level of diversity is highest in natural, unmanaged ecosystems and lowest in areas modified by man (Dajoz 2000).

Species diversity is the most tangible level of biodiversity, being the easiest and most practical of these three levels to recognize, measure and analyze (Stork 1993; Spellerberg 1996a). It is the most common measure of biodiversity, especially when considering conservation (Bond 1989a; Purvis & Hector 2000), and is generally considered the fundamental unit for biodiversity study and analysis (Wilson 1992; Heywood & Baste 1995). Species diversity is the primary focus of this study.

Whittaker (1972) described species diversity at three geographical scales: alpha (α), beta (β) and gamma (γ). Alpha diversity is within-habitat diversity or the diversity of species in a particular habitat or area. Beta diversity is between-habitat diversity or the rate and extent of change in species from one habitat to another. Gamma diversity is within-region diversity, or the diversity of species within a large geographical area, and is a composite of alpha and beta diversity.

1.1.3 Estimating global species diversity

Since the birth of the term ‘biodiversity’ in 1986 there has been an exponential rise in biodiversity research across the world (Wilson 1997). Concern for the present state of local and global environments and grim predictions of biodiversity loss have largely stimulated this growth (Huntley 1989; Heywood & Baste 1995). However, despite this surge of biodiversity research, there is no list or complete inventory of existing species (Spellerberg 1996a) and scientists do not have an even vaguely accurate idea of how many species exist on the Earth today (Huntley 1989; Heywood & Baste 1995). In fact, scientists are finding that only a tiny fraction of the Earth’s biodiversity has been explored (Wilson 1997).

Many scientists have used extrapolation in attempts to estimate the total number of species on Earth (Erwin 1982; Erwin 1988; May 1992; Stone 1993). Current estimates vary widely, from 10 to 100 million species (Wilson 1992; Lovejoy 1997), but 13 million species is a generally accepted approximation (Heywood & Baste 1995). Since only about 1.4 to 1.8 million of these species have been classified and named (Huntley 1989; Stork 1993; Lovejoy 1997), researchers endeavour to fill the huge gap in our knowledge of species biodiversity. Approximately 300 new species are described each day and there is no slowdown in sight (Purvis & Hector 2000). Using even the lowest estimates of global species richness, it would take between 90 and 120 years to describe all of the world's species (Stork 1997). After 200 years of inventory (Stork 1993), the known world species richness is still only a fraction of the actual species richness (Ehrlich & Wilson 1991).

Information regarding species diversity is so poor that there is not a single hectare on Earth where all the biological components are known, even at relatively well-sampled sites (Stork 1993). There are also serious weaknesses in our knowledge of species interactions, distributions and losses (Spellerberg 1996a). Estimates suggest that we know nothing about the distribution of at least 86% of the world's species, 7% of species are known from only one locality and the threatened status is known for less than 0.05% of species (Stork 1997). It is obvious that there is great uncertainty regarding both what is known and not yet known about species diversity (Stork 1993) and research must address these questions.

1.1.4 Invertebrate abundance and diversity

Throughout most of the world, vertebrates are far better known than invertebrates since biodiversity research has largely shown a 'vertebrate chauvinism' (Wilson 1985; Lovejoy 1997). For example, much is known about the distribution, biology and threatened status of birds and large mammals, but similar data for invertebrates are almost nonexistent (Stork 1997). Estimates of global species numbers are so imprecise because inconspicuous taxa, such as invertebrates, have been largely ignored (Primack 2000). Vertebrates also drive many conservation efforts because it is often assumed that if vegetation and 'charismatic megafauna' are protected, the invertebrates will be conserved as well (New 1998, Grove & Stork 1999). However, these assumptions are unwarranted given the vast abundance, biomass and species diversity of the Earth's invertebrates.

Invertebrates dominate all of the world's faunal groups in terms of sheer numbers of individuals and biomass (Black *et al.* 2001). This is particularly true of insects and their close relatives (Samways 1993). According to Wilson (1992), arthropods alone account for over 85% of the total weight of all land animals. The total biomass of soil invertebrates and microorganisms is greater than all of the above-ground vertebrates combined (Edwards 2000). In the United States earthworm and arthropod biomass is estimated at 1000 kilograms per hectare, while all other terrestrial vertebrates combined, including humans, only account for 36 kilograms per hectare (Black *et al.* 2001). Average annual spider abundance in the world ranges from 50 to 150 individuals per square metre, but can reach over 1000 individuals per square metre (Marc *et al.* 1999).

Invertebrates comprise 95% of all described animal species (Brusca & Brusca 1990) and most of the 10 to 100 million species estimated to live on Earth today (Lovejoy 1997) are invertebrates. Over one million terrestrial arthropod species alone have been recognized and Hawksworth & Kalin-Arroyo (1995) estimated that two to 20 million remain to be described. Invertebrates have successfully invaded virtually every habitat on Earth and have exploited every imaginable lifestyle and developmental strategy (Cloudsley-Thompson 1968; Brusca & Brusca 1990). They constitute over 30 phyla (Brusca & Brusca 1990) and include some familiar animals such as spiders, butterflies, snails, earthworms, crabs and flies. Although humans come into direct contact with many invertebrates every day, we have no clear idea of the true richness of global invertebrate diversity (Stork & Eggleton 1992), as only a fraction has been discovered (Ehrlich & Wilson 1991).

Although invertebrate groups are typically diverse, one invertebrate taxon, the arthropods, is 'hyperdiverse,' meaning that it contains more species than expected for a single group (Ehrlich & Wilson 1991; Colwell & Coddington 1994) and most of the undescribed species in the world are arthropods (Stone 1993). Within the Arthropoda, the Insecta are well known to be the most abundant, successful and speciose taxon (Ehrlich & Wilson 1991; Stork & Eggleton 1992; Stork 1997), with about one million known species (Hawksworth & Kalin-Arroyo 1995). However, the described species only account for about seven to 10% of the true species number (Samways 1993) and Stork (1993) estimated that two to 30 million species of insects remain unknown. Importantly, insects also appear to be the group threatened with the greatest number of extinctions (Stork 1997).

In addition to our poor knowledge of global invertebrate species numbers, information on the distribution and vulnerability for known species is lacking. At regional and local levels, there are few data on the turnover of species with distance, altitude and habitat (Stork & Eggleton 1992) and we know little about the biology and habitat requirements of most described invertebrates (Moore 1991). Data on the threatened status of insects and other invertebrates are almost nonexistent (Stork 1997). The United States Endangered Species Act itself fails invertebrates, for it only allows protection of invertebrate species and subspecies, while giving provision for the protection of vertebrate species, subspecies and distinct population segments (Black *et al.* 2001). With the exception of a few spectacular species, soil invertebrates do not appear at all on endangered species lists (Lavelle 1996).

Fortunately, public interest in invertebrates has recently increased, as reflected in the number of guides and popular books that are now available (Kirby 1992). With this interest has come a rising concern for the future of invertebrate biodiversity and a growing recognition of the importance of invertebrate biodiversity research.

1.1.5 Benefits of biodiversity to humans

According to Hunter (1999), biodiversity has both intrinsic value and instrumental value. All species and biological communities have intrinsic value simply because they are part of nature and, regardless of their service to humans or other species, they have a right to exist. This ethic is rooted in most of the world's religions and in many societies and cultures (Gaston & Spicer 1998). Biodiversity's instrumental values, however, are directly linked to its usefulness to other species, including humans, and the benefits derived from its existence.

Some of the important instrumental values and benefits of biodiversity are as follows:

- 1) Economic benefits: Biodiversity provides humans with species for direct consumption, production and industrial use. Part of our existence depends upon the many species that we consume directly as food, fuel, fibres, clothing and shelter (Lovejoy 1997; Patrick 1997) and biodiversity supplies man with a continuing source of these 'marketable commodities' (Mooney *et al.* 1995). In addition, biodiversity provides many raw materials from which marketable goods are

synthesized. For example, great medical advances have been made because of investigations of natural organisms (Lovejoy 1997) and a significant proportion of our medicines are derived from a variety of natural organisms (Gaston & Spicer 1998; Hunter 1999). In fact, about 25% of prescriptions in the United States contain active ingredients with plant origins (Lovejoy 1995) and 25 000 to 30 000 species of plants are used in traditional medicine alone (Heywood & Baste 1995). Further, ecotourism, outdoor recreation, fishing, hunting, bird watching and gardening, all of which involve large sums of money, would not be possible without biodiversity (Gaston & Spicer 1998; Hunter 1999).

- 2) Scientific and educational benefits: Biodiversity provides people with fascinating and inspirational subjects for scientific study and education. These two areas, considered to be vital for improving the well-being of people (Hunter 1999), are greatly enhanced by biodiversity. For example, biodiversity allows humans to investigate and understand evolution, genetics and adaptation (Bond 1989a; Hunter 1999) and advances our understanding of the life sciences (Lovejoy 1997).
- 3) Spiritual and cultural benefits: Biodiversity is used for cultural and religious purposes in a non-consumptive manner all over the world (Mooney *et al.* 1995; Burley 2002) by providing inspiration and raw materials for art, music and literature (Bond 1989a). In addition, many people derive pleasure out of just knowing aspects of biodiversity exist, called 'existence value' (Hunter 1999). In this way, biodiversity provides aesthetic, artistic and spiritual experiences for man.
- 4) Ecological benefits: Healthy ecosystems generate and stabilize soils, purify water, maintain the gaseous composition of the atmosphere, control crop and domestic animal pests, support hydrological, carbon and nutrient cycles and are the sources of nutrients and minerals (Ehrlich & Wilson 1991; Heywood & Baste 1995; Spellerberg 1996a; Patrick 1997; Burley 2002). They also regulate climate and break down pollutants and waste (Primack 2000). These 'free services' are dependent upon biodiversity because it maintains the structure, functioning, stability and sustainability of ecosystems (Barbier *et al.* 1994; Heywood & Baste 1995; Spellerberg 1996a). Biodiversity can also be used to indicate ecological change (Lovejoy 1997). Climate change and environmental degradation can alter levels of biodiversity and, in turn, help warn humans of potentially devastating ecological or climatic alterations. For example, pollution levels in rivers can be monitored using insect species abundance (Spellerberg 1996a) and air and

rainwater pollution can be detected using the composition of lichen communities (Primack 2000). Ecosystem services cannot be provided without biodiversity because ecosystems can only operate efficiently if a high diversity of macro- and microscopic organisms is present (Patrick 1997). Each species is interdependent to some degree and the loss of one part of the ecosystem could lead to instability and eventual collapse of the whole (Bond 1989a).

- 5) Potential benefits: Biodiversity supplies man with future options for consumption, production and other uses, since many species have not even been identified, let alone explored for potential uses (Gaston & Spicer 1998; Hunter 1999). Many uses for biodiversity may only be discovered and developed in the years to come. By conserving present biodiversity, future generations have the option to find uses and values for biodiversity that we do not presently recognize (Gaston & Spicer 1998).

Whether measured in economic, social, aesthetic or moral terms, biodiversity has great importance and value (Heywood & Baste 1995) and must be conserved. However, the issue of biodiversity conservation is very complicated. Economic value is an unavoidable consideration when committing and prioritizing resources for conservation (Heywood & Baste 1995) because it is certain that humans will suffer great economic losses if biodiversity is compromised. However, it is extremely difficult to place economic worth on biodiversity, many aspects will never be adequately captured by market value and biodiversity is perhaps morally beyond value (Burley 2002). This is further compounded by the fact that it is difficult, if not impossible, to determine how much biodiversity can be lost before ecosystems are affected and ultimately cease functioning (Purvis & Hector 2000). Because humanity is so dependent upon biodiversity for health, prosperity and environmental welfare, the loss of ecosystems, populations, species and genes poses a major threat to the survival of humans and other organisms (Barbier *et al.* 1994; Burley 2002).

1.1.6 Global species extinction

Biodiversity has been given recent widespread attention due to the realization that it is disappearing (Wilson 1997) and current rates of species loss are seemingly unsustainable (Purvis & Hector 2000). We are currently losing species 1000 to 10 000 times faster than the rate due to normal evolutionary processes (Wilson 1985; Huntley 1989) and over 99%

of these extinctions are caused by human activity (Primack 2000). However, such extinction estimates are derived from relatively well-studied and conspicuous groups such as flowering plants, mammals and birds, without knowing how these figures pertain to the other 99.9% of species (Heywood & Baste 1995; Primack 2000). It is these other groups, such as invertebrates, that are most likely to be affected by extinctions (Stork 1997). In addition, many undiscovered and undescribed species have gone extinct without our knowledge and these are certainly not recorded (Gaston & Spicer 1998).

However, over 1000 plant and animal species extinctions have been recorded since 1600, about half of which occurred during the past century (Gaston & Spicer 1998). Currently, approximately 11% of bird, mammal and tree species are seriously threatened with extinction, as are many freshwater fishes, molluscs, gymnosperms and palms (Primack 2000). Conservative calculations indicate that species are being lost at a rate of 1% to 5% per decade (Barbier *et al.* 1994) and as much as 25% of the Earth's species present in the 1980's may be extinct by the year 2015 (UNEP 1992). It is important to note that species extinctions do not occur in isolation, but that species associations and interactions are also lost and these affect the ecosystem as a whole (Spellerberg 1996a). This unfortunately suggests that many of the real and potential benefits derived from biodiversity will not be experienced by future generations.

1.1.7 Threats to global biodiversity

Threats to biodiversity come from many sources, but the dominant force causing the alteration, redistribution and loss of biodiversity is human activity (Heywood & Baste 1995; Mooney *et al.* 1995). The global implications and scale of destructive human activities have only recently been widely appreciated and the consequences are now substantially threatening humans economically and culturally (Mooney *et al.* 1995). Only now have we begun to realize the great power that humans have to influence and modify our environment and the course of evolution (Younes 1996). It is clear that terms such as 'undisturbed' and 'virgin forest' are only relative, since no part of world is truly untouched by humans (Heywood & Baste 1995) and as the human population continues to grow, pressures on biodiversity will surely increase. Some specific threats to biodiversity include habitat destruction, the introduction of non-indigenous species, pollution and climatic change.

By far, the largest threat to the world's biodiversity is habitat destruction, including habitat degradation, fragmentation, isolation, conversion and edge effects (Ehrlich & Wilson 1991; Lovejoy 1997), which is directly due to centuries of agriculture, silviculture, road building, industrial development and urbanization (Heywood & Baste 1995). Habitat loss and modification are occurring at alarming rates, causing reduced ecosystem complexity and biodiversity and changes in species interactions (Barbier *et al.* 1994; Mooney *et al.* 1995). This trend is particularly evident in forest ecosystems, both temperate and tropical. Because they are largely located in the same areas of modern western society, temperate and broadleaf evergreen forests are severely affected by continuous clearance for settlement and agriculture that has been practiced in some locations for centuries (Meadows 1985; Mooney *et al.* 1995). Tropical forests are regularly lost, degraded and fragmented for timber products or conversion to pastures, cropland and plantations (Mooney *et al.* 1995; Spellerberg 1996a). The best estimates indicate that 11 million hectares or 1.8% of tropical forest are deforested annually (Huntley 1989; Myers 1989; Mooney *et al.* 1995). Twenty-five to 40% of tropical forests have already been lost due to human exploitation (Erwin 1988) and projections from current deforestation rates indicate that there will be very little intact tropical forest after 2040 except in small, protected areas (Primack 2000).

Another major threat to global biodiversity is the introduction of non-indigenous species (Spellerberg 1996a; Lovejoy 1997; Denslow 2002) through international travel and trade, agriculture, horticulture and climatic variation (Mooney *et al.* 1995; Primack 2000). Although introductions may appear to increase regional biodiversity, they also tend to homogenize biodiversity between regions (Gaston & Spicer 1998) and lower local biodiversity (Hawksworth & Kalin-Arroyo 1995). Alien species in new environments often have no predators, effective competitors or diseases and generally occur at high population densities (Carroll & Hoffman 2000). As a result, invasive alien species can transform habitat, out compete, displace and prey on native species, alter ecosystem processes and change functional relationships, microclimate, soil chemistry and fire regimes (Breytenbach 1986; Gaston & Spicer 1998; Huntley 1999; Denslow 2002), all to the detriment of the indigenous biodiversity. Habitat destruction also contributes to this problem because disturbed or stressed areas are particularly vulnerable to the establishment of alien species (Denslow 2002). Islands and habitats with relatively few species are also

vulnerable (Mooney *et al.* 1995). Whether deliberate or accidental, introduced species present a very severe problem throughout the world (Lovejoy 1997).

Air, water and soil pollution also account for biodiversity losses, especially on a regional scale. Pollution sources include pesticides, chemicals, petroleum wastes and sewage from domestic, agricultural and industrial sources, emissions from factories and automobiles and sediment deposits from eroding logged or farmed hillsides (Primack 2000). Pollution is perhaps the most subtle and universal form of habitat degradation, but it is able to change the environment, stress biological communities, affect trophic dynamics and greatly alter biodiversity (Mooney *et al.* 1995; Lovejoy 1997; Primack 2000). For example, as river pollution increases, insect species diversity declines until there are only a few resilient species left (Spellerberg 1996a).

Climatic change, caused by increasing levels of greenhouse gasses in the atmosphere, also has serious implications for biodiversity (Lovejoy 1997). Burning fossil fuels and forests release carbon (usually as carbon dioxide) and other ‘greenhouse gasses’ into the atmosphere in an unnaturally short geological time (Stork 1993; Lovejoy 1997), creating an enhanced ‘greenhouse effect’ and global warming (Primack 2000). These growing concentrations of greenhouse gases will ultimately cause the temperature of Earth to increase, climates to change and sea levels to rise (Stork 1993; Primack 2000). The crisis is compounded by vehicle emissions, agriculture and tropical deforestation (Mooney *et al.* 1995). These global changes will upset the intricate web of factors upon which biodiversity depends (Lovejoy 1997) and the composition and distribution of biodiversity will be affected (Stork 1993).

The ultimate cause of all of these threats to biodiversity is the continuing exponential growth of the human population beginning in the last century. There are approximately 5.7 billion people on Earth (Gaston & Spicer 1998) and roughly 100 million new people are added to the population each year (Lovejoy 1997). This growth has greatly increased economic activities, development, urbanization and resource exploitation (Barbier *et al.* 1994; Lovejoy 1997). Currently humans use or waste 40% of the total net primary productivity of the terrestrial environment (Primack 2000). Per capita consumption in the industrial world is enormous and unsustainable and our influence on the Earth’s systems is growing exponentially along with the population (Heywood & Baste 1995). In developing

areas including Africa, poverty, exacerbated by population growth, is a prime force affecting biodiversity (Biodiversity Support Programme 1993).

Biodiversity loss, unlike some pollution and ozone depletion, cannot be reversed (Wilson 1997). As a result, biodiversity conservation is now widely regarded as one of the most urgent and important environmental issues today. It will be a major challenge to address and control the threats to biodiversity.

1.2 FOREST BIODIVERSITY

1.2.1 Global forests & biodiversity

Forest ecosystems vary widely throughout the world and can be categorized into broad global biomes such as boreal or northern conifer forests, temperate deciduous or mixed forests, temperate rain forests, tropical rain forests, tropical deciduous forests and tropical dry or scrub forests (Meadows 1985; Burley 2002). Within these categories, there are a range of more specific forest types, each with its own characteristic faunal and floral components and unique assessment and management needs (Burley 2002).

Forest biodiversity is the variation of all life within the forests, including all of the plants, animals and microbes (Burley 2002). The diversity of forests is great and the vast majority of the estimated 10 to 100 million species on Earth occur in forests (Barbier *et al.* 1994). In particular, tropical forests are the best-recognized concentration of the world's diversity (Lovejoy 1997), are the most complex vegetation type on Earth, are the most productive of the biomes (Meadows 1985) and are important centres of endemism (Spellerberg 1996a). Here species numbers well exceed those of temperate climate zones (Kanashiro *et al.* 2002). Some 50% of all vertebrates, 60% of plant species and possibly 50 to 90% of the world's total species are found in tropical forests (Lovejoy 1997; Reid and Miller 1989; Stone 1993; Primack 2000; Burley 2002). This amounts to at least three million species, but the true number could be ten or more times greater than this estimate (Raven 1988). Tropical forests are likely home to thousands, perhaps millions, of undescribed species of less studied taxa such as insects, nematodes, protozoans and plants (Kanashiro *et al.* 2002).

Because they are home to such a large number of species, it may be surprising that tropical forests comprise only about 7% of the total land surface of the earth (Stone 1993; Lovejoy 1997; Primack 2000). The Tropical Forest Resources Assessment (TFRA) estimated the area of natural forests to be 1756 million hectares in 1990, or about 36% of the total land area of the tropics (Barbier *et al.* 1994). The largest extent of tropical forest is found in Latin American and the Caribbean (918 million hectares), followed by Africa (528 million hectares), then Asia and the Pacific (311 million hectares) (Barbier *et al.* 1994).

Our current knowledge of forest biodiversity is still very limited (Mooney *et al.* 1995) and much still remains to be discovered about the identity and interactions of animal, plant and microbial forest species (Burley 2002). Only about 500 000 tropical and subtropical species are named and catalogued (Raven 1988) and a complete species inventory of a single tropical ecosystem does not exist (Lugo 1988). Forests are complex in structure and contain many types of habitats, each with unique faunal components. For example, the assemblage of life in the tropical forest canopy is entirely different from that of the forest floor. The two habitats share only one common species – the trees themselves (Lovejoy 1997). According to Erwin (1988), most of the undescribed species of arthropods in the world will be found in tropical forest canopies.

Because of their great species richness, complexity and importance in maintaining the world's species diversity, any discussion of biodiversity must include forests.

1.2.2 Forest invertebrate abundance and diversity

Despite our poor understanding of invertebrate species, some general patterns of world invertebrate distribution have been recognized. Most of the world's invertebrate species diversity is found in terrestrial environments and the greatest diversity occurs in the tropical forests, where five to ten times more invertebrate species occur than in temperate environments (Stork & Eggleton 1992). In fact, the overall high levels of tropical forest species diversity are primarily due to the great diversity of invertebrates (Primack 2000). An immense species diversity of invertebrates can occur in a single small forest patch (Grove & Stork 1999) or even in a single small habitat within a forest. For example, more than 4000 species of arthropods were collected from only 10 trees in Borneo (Stork 1991) and 1200 species of beetle were collected from a single tree in Panama (Erwin 1982). If

estimates are correct, 90% of the world's species may be tropical forest insects (Primack 2000).

Because of their generally small size and cryptic behaviour, invertebrates often go unnoticed in forest communities. However, their abundance fully compensates for their small size and their biomass is usually greater than that of vertebrates (Dajoz 2000). Many studies have shown that insects account for the highest faunal biomass in forests, reaching several tons per hectare, compared to the few kilograms of mammals and birds (Dajoz 2000). Stork (1988) examined the abundance of tropical forest invertebrates in Indonesia and estimates that one hectare of forest contains 42.5 million arthropods, of which 23.7 million live in the soil, 6.0 million in the litter, 0.1 million in the herbaceous layers, 0.5 million on tree trunks and 12.0 million live in the canopy. A study in a German oak and beech forest found that the abundance of winged insects is 4123 individuals per square metre, with a biomass of 14.321 kilograms per hectare (Dajoz 2000). Ants and termites are known to comprise as much as 25% of all animal biomass in the Amazon (Samways 1993).

Forests are able to support such great abundance and species diversity largely due to their climate and structure. Forests are generally damp by nature and many terrestrial invertebrates are restricted to relatively moist areas and microhabitats (Brusca & Brusca 1990). Indigenous forests are also very complex in structure and provide a vast range of microhabitats and a multitude of niches for invertebrates to exploit (Endrody-Younga 1989). In particular, insect species diversity increases as the structural diversity of vegetation increases (Dajoz 2000). The high diversity of plant species in forests also encourages a high number of invertebrate species because the diversity of one group of organisms can promote the diversity of associated groups (Purvis & Hector 2000). Further, forests are relatively stable environments and climatic variations in forests are usually low and predictable, offering opportunities for specialized invertebrate species that cannot tolerate climatic or resource fluctuations (Dajoz 2000).

Tropical forests contain more diversity than any other environment and most of the species are invertebrates. However, no complete inventory exists of forest invertebrate fauna (Dajoz 2000). It is not surprising that many invertebrate forest species are unknown to science, as few insect and other arthropod species sampled in tropical forests can be found in existing collections or in the world's literature (Raven 1988; Stork 1997). This is in

contrast to temperate environments where it is quite unusual to find a new species of invertebrate (Stork 1997). Due to the alarming rate of forest destruction, it is vital that forest species, especially invertebrates, are catalogued immediately (Erwin 1988).

1.2.3 Why study forest invertebrates?

The diversity of forest invertebrates is so vast and unique that it alone warrants their study. However, there are many additional reasons why forest invertebrates are useful subjects for research. These include their roles in ecosystems, their specialization, vulnerability to extinction and potential as environmental indicators.

Invertebrates play vital roles in the functioning of forest ecosystems. Some of these roles include:

- 1) Herbivory: Herbivory (eating plant material) by animals, including invertebrates, influences the structure and composition of vegetation (Burley 2002). Invertebrates consume flowers, fruits, foliage and seeds, which affects the population dynamics, dispersal and regeneration of trees (Dajoz 2000; Burley 2002; Armstrong 2002).
- 2) Predation: Predators and parasitoids regulate populations and keep outbreaks of pest species in check (Dajoz 2000; Burley 2002). For example, parasitoids in the genus *Aphytis* prey upon diaspidid scale insects that otherwise can over-exploit and completely destroy their plant resources (Samways 1993)
- 3) Pollination: Pollination of plants by invertebrates and other animals is crucial to the functioning of ecosystems, including forests, and the perpetuation of food webs (Kevan 1999; Black *et al.* 2001). Insects are the main pollinators in tropical forests, where wind pollination is rare (Dajoz 2000).
- 4) Soil maintenance: Invertebrates are vital components of forest soils and can determine their productivity by enhancing microbial activity, accelerating decomposition, regulating the intensity of carbon and mineral recycling and mediating transport processes (Brown 1991; Stork & Eggleton 1992). Insects, worms, mites and other detritivores break down organic waste materials and release it as minerals usable to plants and other organisms (Primack 2000; Black *et al.* 2001).

In addition, many of the yet undiscovered species of invertebrates may have functions or uses still unknown (Burley 2002).

Many forest invertebrates are highly specialized and local and regional endemism is common. Many invertebrate genera and species are confined to the forest biome or are totally dependent upon forests for at least one stage of their lives (Geldenhuys & MacDevette 1989). Many species of invertebrates are very specific in the resources that they exploit, such as feeding upon a single species of plant (Geldenhuys 1993) or even on a particular part of a certain plant species, and others have very precise habitat requirements (Kirby 1992). In some forests, entire invertebrate communities may be dependent upon water-filled tree cavities, for example (McComb & Lindenmayer 1999). Such specialization allows whole invertebrate populations to be sustained by small areas and relatively few resources (New 1998).

Many forest invertebrate species and groups are vulnerable to extinction. According to Primack (2000), ecologists have recognized 14 specific categories of species that are particularly susceptible to extinction and must be carefully monitored and conserved. The following is a list of these categories that apply to many forest invertebrate groups:

- 1) Species with narrow geographical ranges
- 2) Species with only one or a few populations
- 3) Species that are not effective dispersers
- 4) Species with specialized niche requirements
- 5) Species that are characteristically found in stable environments
- 6) Species that form permanent or temporary aggregations

Because at least six of the 14 recognized categories pertain to many forest invertebrate groups, such species must be considered to be at great risk of extinction.

Invertebrates are useful as indicators of environmental change and habitat disturbance due to a variety of characteristics. Many invertebrates have very limited powers of dispersal (Kirby 1992) and cannot move easily to new areas when conditions are altered. Invertebrates often have very specialized diets, habits or habitat requirements that may vary according to life stage (Moore 1991) and any alteration in the environment that affects these needs will be reflected in changes in invertebrate populations. In addition, most invertebrates have annual life cycles or even have two or more generations in a year and specific conditions must be present each and every year to successfully breed (Kirby 1992). All of these factors cause invertebrates to be much more sensitive to habitat change than most plants or vertebrates (Desender *et al.* 1991; Kirby 1992; Kotze & Samways

1999a). This sensitivity is compounded by the fact that invertebrates, particularly insects, can have complex life cycles and each different stage may have different habitat requirements (Kirby 1992). Further, invertebrates are usually small and spend much of their lives in a specific microhabitat and microclimate (Kirby 1992). As a result, problems in conservation are often first seen in invertebrates (Dempster 1991), even minor habitat disturbance or climate change can prove to be significant (Kirby 1992) and invertebrates can alert humans to larger or growing environmental issues.

1.3 SOUTH AFRICAN FORESTS

1.3.1 Description of South African forests

There are seven recognized terrestrial biomes comprising 68 general vegetation types found in South Africa (Low & Rebelo 1996). Of these seven, forest is the smallest biome, covering just more than 2000 square kilometres or 0.1% of the land area of South Africa (Geldenhuys 2000), but it is also the most widely dispersed of all the biomes (Geldenhuys & Knight 1989). In fact, forest patches can be found within almost all of the other South African biomes (Midgley *et al.* 1997).

South African forests occur as a series of scattered patches along the eastern and southern margins of the country (Geldenhuys & Knight 1989; Midgley *et al.* 1997). Forests are found in the coastal belt from the Cape Peninsula eastwards through the Outeniqua and Tsitsikamma Mountains of the southern Cape, have a discontinuous distribution through the midlands of the Eastern Cape and KwaZulu-Natal and extend northwards along the Drakensberg mountains from KwaZulu-Natal to the Soutpansberg mountains in Limpopo Province (Geldenhuys & MacDevette 1989; von Maltitz *et al.* 2003). There are several large forest complexes, but these are separated by zones of only small, highly fragmented and isolated forest patches or zones of no forest at all (Geldenhuys & MacDevette 1989). The distribution of South African forests and the associated altitudes are shown in Figure 1.1. Most forest patches are less than one square kilometre in area, with larger patches only common along the Cape Garden Route and the northern Drakensberg escarpment (Geldenhuys & Knight 1989; Low & Rebelo 1996).

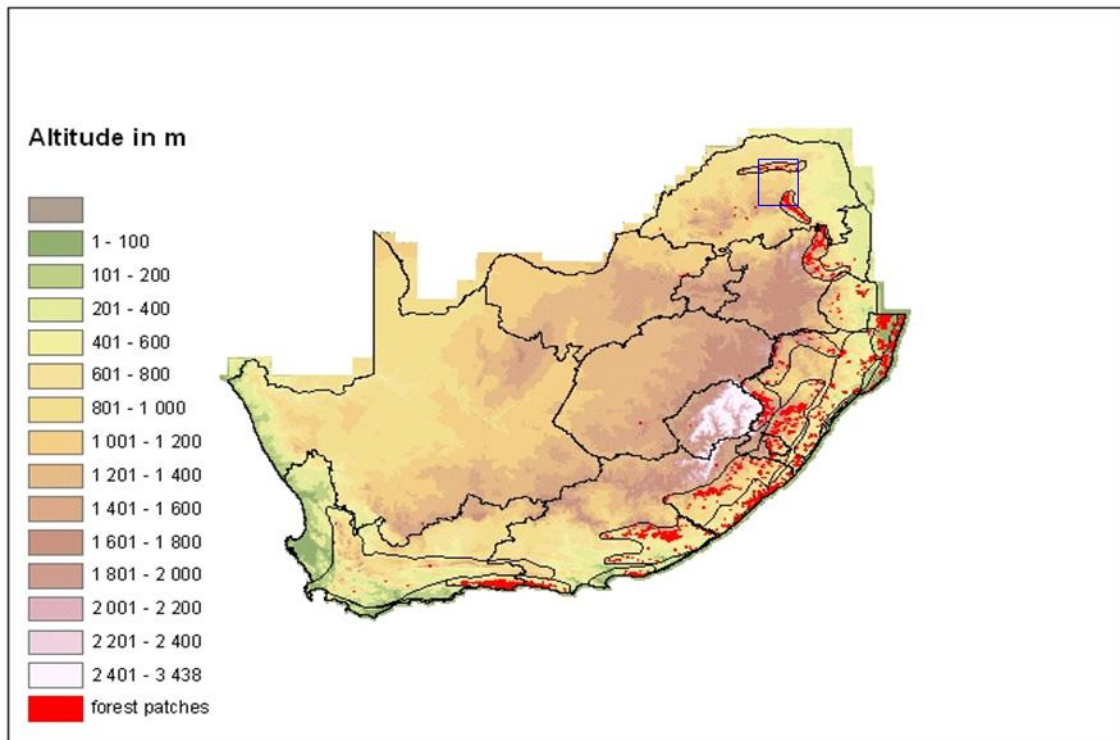


Figure 1.1: Altitudinal distribution of South African forests (from von Maltitz *et al.* 2003). The area covered in this study is demarcated in blue.

In the South African context, ‘forest’ is defined as follows:

A generally multilayered vegetation unit dominated by trees (largely evergreen or semi-deciduous) whose combined strata have overlapping crowns (i.e. the crown cover is greater than or equal to 75%), and where graminoids in the herbaceous stratum (if present) are generally rare. Fire does not normally play a major role in forest function and dynamics except at the fringes (Bailey *et al.* 1999; von Maltitz *et al.* 2003).

The closed canopy of South African forests creates reduced light levels in the subcanopy area where epiphytes, ferns and lianes can be common (Rutherford & Westfall 1994). The dense plant cover protects the forest and reduces soil erosion, but also prevents most ground layer vegetation growth (Rutherford & Westfall 1994; Low & Rebelo 1996). Due mainly to their humid nature, fire rarely effects forest interiors except under extremely hot and dry conditions (Low & Rebelo 1996), but fire is important to the forest margin communities (Huntley 1984) and can greatly influence forest boundaries and distribution (Geldenhuys 1994; Midgley *et al.* 1997). South African forests are distinguished from closed canopy moist savannas by the absence of C4 grasses and the lack of fire in the interior (Huntley 1984; Geldenhuys 2000).

The plants of South African forests have affinities to the tropical forest flora and they are strongly related to the lowland Guineo-Congolian and upland Afromontane forests of tropical Africa (White 1983; Huntley 1984; Geldenhuys & MacDevette 1989). Elements of both of these forest types tend to intergrade over much of the South African forest biome (Huntley 1984).

According to von Maltitz *et al.* (2003), although forests are able to modify their own substrate to some extent, most South African forests are found on nutrient poor soils but are able to grow on rich substrates as well. Soils supporting forests are derived from a variety of substrates, including quartzitic sandstones, mudstones, shales, schists, Aeolian sands, conglomerates and dolerite sand granite-gneiss (Geldenhuys *et al.* 1986; Geldenhuys 2000).

Water availability limits the area of South African forests (von Maltitz *et al.* 2003) and forests are generally restricted to locations with a mean annual rainfall of more than 525 millimetres in winter rainfall regions and more than 725 millimetres in regions with

summer rainfall (Rutherford & Westfall 1994; Low & Rebelo 1996). Disturbance factors, especially the occurrence of fire, also have a major impact on forest distribution (Geldenhuys 1994; von Maltitz *et al.* 2003). Elevation and temperature are not important influences on South African forest distribution, since forests occur from sea level to over 2100 metres in altitude (Rutherford & Westfall 1994; Low & Rebelo 1996) and from the snow and frost prone Drakensberg to the hot KwaZulu-Natal coastal plain (von Maltitz *et al.* 2003).

1.3.2 South African forest classification

All South African forests are essentially evergreen and share similar floristic community structure and composition. However, because South African forests are found across the landscape in regions of varying rainfall, temperatures, altitude, latitude and topography, there is a diversity of forest vegetation types across South Africa (Adamson 1938; von Maltitz *et al.* 2003).

Over the years many authors have produced classification systems for South African forests (see Adamson 1938; White 1978; White 1983; Acocks 1988; Rutherford & Westfall 1994; Low & Rebelo 1996; Geldenhuys 2000), but none has been accepted nationally (von Maltitz *et al.* 2003). Although almost all existing classifications recognize the main differences in forest types based on their origin and characteristic species, South African forest classification has been primarily subjective (based on the amount and quality of merchantable timber), was based on parochial systems or has used spatial scales too narrow for meaningful interpretation within a wider context (von Maltitz *et al.* 2003). None of the existing forest classification systems have been objectively derived from biological data and interest in some areas, particularly Mpumalanga and Limpopo Province, has been limited (von Maltitz *et al.* 2003).

Forest classification is important since it is used for conservation area planning and biomonitoring, in operational planning and utilization management and to direct research priorities (Geldenhuys & Venter 2002). Therefore, it was necessary to coordinate a nationally accepted and objective classification system for all forests in South Africa. To help unify information and clearly define and map South Africa's forest types, in 2003 a team of forest specialists analyzed available floristic and faunal data and presented a

formalized biogeographic-floristic classification of South African indigenous forests in a report entitled ‘Classification System for South African Indigenous Forests’ (von Maltitz, *et al.* 2003). This new classification system delineates seven major forest groups, comprising 20 zonal and intrazonal forest types, and four azonal forest types. This is in contrast to past classification systems such as Low and Rebelo (1996), which divided the South African forest biome into only three vegetation types: Afromontane, Coastal and Sand Forest. The new classification system proposed by von Maltitz *et al.* (2003) will be followed in the present study.

Although existing South African forest classification systems vary considerably, forests have been consistently divided into two categories: 1) inland temperate Afromontane forests and 2) coastal subtropical Indian Ocean types (Huntley 1984; Low & Rebelo 1996; Midgley *et al.* 1997). Based on tree species composition, Afromontane forests appear distinct from coastal forests (Geldenhuys 1992). The lack of consensus between classification systems relates to finer subdivisions within Afromontane and coastal forest types (von Maltitz *et al.* 2003). Four of von Maltitz *et al.*’s (2003) major forest groups (comprising 12 forest types) can be broadly classified as South African Afromontane forests: (1) the Southern Afrotropical Group, (2) the Northern Afrotropical Group, (3) the Northern Mistbelt Group and (4) the Southern Mistbelt Group.

1.3.3 South African Afromontane forests

Afromontane forests occur in six provinces of South Africa (Low & Rebelo 1996, Table 1.1). Patches of Afromontane forests are found along mountain chains, but are only extensive on the east- and south-facing slopes (Low & Rebelo 1996). They are also found as small patches on north- and west-facing slopes, but only in ravines or below steep cliffs (Adamson 1938; von Maltitz *et al.* 2003). This distribution is mainly the result of moisture availability, since this forest type generally requires a high and evenly distributed moisture supply (Low & Rebelo 1996; von Maltitz *et al.* 2003). Rainfall is usually greater than 700 millimetres per year in areas supporting Afromontane forest and, in northern regions, 80 to 85% of this rain falls during the summer (Adamson 1938; Low & Rebelo 1996). Mists, which are an important contributor of additional moisture in a number of forests, occur so frequently that Afromontane forests are sometimes called ‘Mistbelt Forests’ (Adamson 1938; von Maltitz *et al.* 2003). South-facing mountain slopes, where Afromontane forest

is most sizeable, provide the maximum effect of the south-westerly and south-easterly wind-driven rains and moisture is therefore higher (Low & Rebelo 1996). Forests do not normally occur on northern slopes that fall within the rain shadow (van Wyk & Smith 2001). Fires also confine Afromontane forests to specific parts of the landscape (Geldenhuys 1994).

Table 1.1: Afromontane forest by province in South Africa. The total area of the Afromontane forest in each province, the proportion of the province area that Afromontane vegetation occupies and the contribution to the total area of Afromontane forest in South Africa are given (Low & Rebelo 1996).

<i>Province</i>	<i>Area (km²)</i>	<i>Proportion of province (%)</i>	<i>Proportion in South Africa (%)</i>
Limpopo Province	242	0.20	4.12
North-West Province	0	0	0
Western Cape	1688	1.30	28.73
Gauteng	0	0	0
Mpumalanga	365	0.47	6.22
KwaZulu-Natal	792	0.84	13.48
Eastern Cape	2795	1.64	47.55
Free State	68	0.05	1.16
Northern Cape	0	0	0

Because of altitude, latitude and proximity to the coast, temperatures within Afromontane forests are generally low and consistent (von Maltitz *et al.* 2003). Unlike other South African forest types, Afromontane forest can occur at elevations from sea level to 1500 metres and above (Huntley 1984; Low & Rebelo 1996). The Afromontane forests of Knysna, for example, are found from the coast to 1000 metres and are similar to the montane forests of southern and East Africa (Meadows 1985). In this case, the southern latitude apparently compensates for the low altitude (Meadows 1985; von Maltitz *et al.* 2003). The upper limits of Afromontane forests are generally dependent on the heights of the mountains themselves (Adamson 1938).

Afromontane forest soils are generally well developed and mature (Low & Rebelo 1996). However, the soils in mountainous forests can be shallow and immature, since soil depth

usually decreases with altitude (Meadows 1985) and most forests are found on steep slopes (Adamson 1938; Low & Rebelo 1996). In addition, soils may be leached in areas with high precipitation (Low & Rebelo 1996).

A closed main canopy, multi-layered vegetation and irregular exterior (Adamson 1938; Geldenhuys & Knight 1989) characterise the vegetation of Afromontane forests. The main canopy is not uniform in height, with emerging trees reaching 30 to 40 metres (Rutherford & Westfall 1994; Low & Rebelo 1996). Within forests there are distinct strata of emergent trees, canopy trees and shrub and herb layers (Rutherford & Westfall 1994; Low & Rebelo 1996). Common tree genera include *Podocarpus*, *Ilex*, *Olea*, *Pittosporum*, *Rapanea* and *Xymalos* (Huntley 1984; Geldenhuys *et al.* 1986). Characteristic tree species include yellowwoods *Podocarpus falcaus* (Thunb.) R. Br. Ex Mirb. and *Podocarpus latifolius* (Thunb.) R. Br. Ex Mirb., ironwood *Olea capensis* L., Cape beech *Rapanea melanophloeos* (L.) R. Br., stinkwood *Ocotea bullata* (Burch.) Baill. and sneezewood *Ptaeroxylon obliquum* (Thunb.) Radlk. (Meadows 1985). Ferns and herbaceous plants are also common (Low & Rebelo 1996).

1.4 PURPOSE AND OBJECTIVES

The forests of South Africa are one of the most vulnerable vegetation types in the country (von Maltitz *et al.* 2003). Because South African forests are used by humans for a variety of services and products, they must be protected from overexploitation. In an attempt to balance human needs with forest health and to promote their sustained use, conservation and management policies have been drafted for South African forests (McKenzie 1988). However, wise conservation planning is impossible without information on the species involved (Spellerberg 1996b) and little is known about South African forest species and the processes that may determine the survival of forest biodiversity. Although management policies for the southern Cape forests are based on detailed ecological studies, fewer comprehensive studies have been completed in other South African forests (C. J. Geldenhuys 2003, pers. comm.). As a result, guidelines for South African forest management are often based on assumption and incomplete knowledge. Without solid scientific information on the underlying biodiversity, management and conservation policies may be misguided (Stone 1993).

Generally, forest research in South Africa has not moved much beyond the descriptive phase because forests are small in area, have great economic value and most are situated far from major universities (Midgley *et al.* 1997). Recruitment, growth and mortality, the dynamics of indigenous and invader species and nutrient cycling have been investigated in South African forests (C. J. Geldenhuys 2003, pers. comm.), but these studies all focused on forest flora. There have been very few studies to investigate richness, (Geldenhuys & MacDevette 1989) distribution patterns, organism interaction and endemism in forest species (Midgley *et al.* 1997), particularly with regards to fauna. There is an urgent need for research to help provide guidelines for forest conservation, while addressing and allowing sustainable use of forests (Midgley *et al.* 1997).

Invertebrates in particular are largely overlooked in forest research. Until recently, the needs of invertebrates have received little attention, even world-wide (Kirby 1992). A literature search completed by Kotze and Samways (1999b) showed only 12% of studies conducted in Afromontane-type forests mentioned invertebrates. Insects and other invertebrates are also largely overlooked when forest management issues are discussed, mainly because there are so many species, they are taxonomically problematic and are so poorly known (Grove & Stork 1999).

This study will help to fill the growing need for information regarding South Africa's indigenous forest biodiversity and the largely ignored invertebrate fauna. This study examines the species diversity and distribution patterns of selected invertebrates in Limpopo Province indigenous forests. It also assesses various invertebrate diversity surrogates and provides recommendations for invertebrate conservation and management.

Chapter 2 describes the forest sites examined in this study, the invertebrate taxa investigated and the collection methods used.

Chapter 3 describes the composition, richness, diversity and evenness of target invertebrate taxa in Limpopo Province forests and comparisons are made between forest regions and individual forests. The factors that influence the richness of target invertebrates in Limpopo Province forests are evaluated and introduced invertebrate species are also discussed.

Chapter 4 focuses on the distribution and biogeographic patterns of target invertebrate taxa in Limpopo Province forests. The distributions and patterns of endemism in target invertebrate groups are evaluated and similarity analyses between forest regions and individual forests are presented. Forest history and some current biogeographic theories are also discussed.

Chapter 5 assesses surrogates and indicators of target invertebrate diversity in Limpopo Province forests. Individual invertebrate taxa, plant and bird species richness are evaluated as indicators of target group species richness and the higher taxa and morphospecies methods are examined as surrogates for invertebrate species richness. Land classes are assessed as surrogates for the target group species' compositions of forests.

Chapter 6 summarises this study and presents invertebrate conservation recommendations for Limpopo Province indigenous forests.

CHAPTER 2

STUDY SITES, TAXA AND METHODS

2.1 INTRODUCTION

2.1.1 Northern Mistbelt Forests of Limpopo Province

Von Maltitz *et al.* (2003) classified the indigenous mountain forests of Limpopo Province as Northern Mistbelt Forests (forest type III1) within the Northern Mistbelt Group (group III). Occurring on the slopes of the high mountains, these forests are distributed as linear archipelagos, from north to south in the Drakensberg and east to west in the Soutpansberg. Forests are most extensive on the wet east-facing slopes of the Drakensberg escarpment and are confined to the south- and east-facing slopes of the Soutpansberg (Adamson 1938; van Wyk & Smith 2001).

The following description of the Northern Mistbelt Forests of Limpopo Province was obtained from the ‘Classification System for South African Indigenous Forests’ (von Maltitz *et al.* 2003), unless otherwise noted.

Northern Mistbelt Forests are found at altitudes of 700 to 1800 metres from the tops of mountains to the foothills and down into savannah vegetation along river systems. They can occur on gentle to steep slopes, below cliffs, in narrow gullies or in open valleys. Forest temperatures range from below zero to above 30 °C according to season and altitude. Most of the annual precipitation (between 600 and 1800 millimetres) occurs between November and April and forests at altitudes over 1050 metres also receive ‘fog drip’ from frequent mists.

Soils in the area of Northern Mistbelt Forests are derived from a variety of formations, but they are generally sourced from sandstone, basaltic or quartzitic substrates and are usually highly weathered, red ferrallitic soils with a high clay fraction. However, shale, lava, tuff, siltstone, mudstone, conglomerate and dolerite are also found in the area (van Wyk & Smith 2001).

The Northern Mistbelt Forests of the Limpopo Province have been further classified along the altitudinal gradient into three ecological subtypes: mistbelt forest, semi-deciduous scrub forest and semi-deciduous mixed forest. Mistbelt forest is typically found at higher altitudes, has a high (15 to 25 metres) closed canopy dominated by strangler figs *Ficus craterostoma* Warb. ex Mildbr. & Burret and *Xymalos monospora* (Harv.) Baill. and has a dark and moist interior. At least one or two sub-canopy tree layers are present and the understory can be open to densely vegetated. Shrubs are usually present in the understory of mistbelt forests, but herbs are absent or poorly developed. Semi-deciduous scrub forest is common at lower altitudes, has a lower (average three to six metres) open canopy with a high proportion of deciduous trees and has an unclear sub-canopy. However, the shrub and herb layers are defined and these layers have a high proportion of grasses. Common trees include *Acacia ataxacantha* DC., *Catha edulis* (Vahl) Forssk. ex Endl. and *Heteropixis natalensis* Harv. This forest subtype is often regrowth forest on former woodland or grassland. Semi-deciduous mixed forest is most often found at the higher reaches of main river systems, is intermediate in height (10 to 15 metres) and has at least one sub-canopy layer and both shrub and herb layers. The broken canopy is dominated by *Albizia adianthifolia* (Schumach.) W.F. Wright.

All of these forest subtypes are subjected to disturbance by windfalls, landslides and lightning strikes. Although fires do not normally affect mistbelt forest interiors, the semi-deciduous scrub subtype is prone to disturbance by fire.

Northern Mistbelt Forests are important biologically since they contain both Afrotropical and Afrotropical elements. For example, these forests share 43% of woody species and 47% of herbaceous species with the southern Cape forests. The semi-deciduous scrub and mixed subtypes also contain a savannah tree species component. Two important regions of floristic endemism occur in the region, the Soutpansberg Centre and Wolkberg Centre, and both contain Northern Mistbelt Forests (van Wyk & Smith 2001).

The Conservation Forestry Section of the Department of Water Affairs and Forestry (DWAF) is responsible for the conservation and management of the indigenous forests in the Limpopo Province in terms of part two of the National Forests Act (Act No. 84, 1998). This includes the Northern Mistbelt Forests of the Soutpansberg and Drakensberg.

2.1.2 Species vs. morphospecies in biodiversity studies

Invertebrate biodiversity studies are notoriously difficult. This is partly due to the fact that species level identification of specimens is problematic, even for an expert. Most major invertebrate groups are not difficult to separate, but species identification is very complex, demanding and specialized (Stork & Eggleton 1992; New 1998) and many specimens have to be sent to experts for identification (Kirby 1992). Identification keys, when they exist, are designed for use by other taxonomists, are often incomplete, outdated and unreliable and there are few invertebrate taxonomists available to identify specimens (Stork & Eggleton 1992; New 1998).

In an attempt to improve the efficiency of invertebrate biodiversity studies, morphospecies are often used in place of formal species to measure biodiversity (Oliver & Beattie 1996a; Slotow & Hamer 2000). Unlike formal species, morphospecies are separated by non-specialists to consistently recognizable units using only superficial external morphological features (New 1998; Pik *et al.* 1999). When properly used, the morphospecies approach has been shown to provide accurate estimates of true species richness in some cases (Oliver & Beattie 1993; Oliver & Beattie 1996a; Pik *et al.* 1999). However, there are several disadvantages to using morphospecies that are relevant to this study.

First, the accuracy of morphospecies identification is questionable. Many formal species of invertebrates are distinguished from others by minute or internal structures and must be dissected and examined by a specialist for identification (New 1998). As a result, when identification is based on appearance, a single morphospecies may actually comprise several valid species (Stork 1997). Further, invertebrate individuals of the same species may appear quite dissimilar depending upon age, sex, location and life stage. Males, females and juveniles of the same species may not resemble each other and could easily be considered separate species (New 1998; Slotow & Hamer 2000). Specimens collected from various parts of a species' range can also show variation (Stork 1997), as do individuals of a polymorphic species (New 1998). Some species may be identified by a combination of characters, some of which can be absent in some individuals (Bisby 1995). When using morphospecies, these discrepancies may result in some degree of splitting and lumping of formal species (Pik *et al.* 1999) and undermine the accuracy of biodiversity measurement.

Second, morphospecies provide no distribution, endemism or interaction information. For example, a site may appear special due to a large number of morphospecies, but all of these may be widespread and common (Slotow & Hamer 2000). Likewise, another site may have few morphospecies, but all could be local endemics or quite rare. Further, no information can be gathered about organism associations or ecological interactions in an assemblage when using morphospecies (New 1998).

Finally, morphospecies cannot be used when comparing more than one site or when monitoring disturbance. Morphospecies from two different sites may appear to be the same, but this assumption cannot be made without the formal species identification. According to Slotow & Hamer (2000), the number of morphospecies present at a site may not change over time even if the true species composition has been altered. Specialized and locally endemic species might be replaced with widespread and tolerant species. Morphospecies inventories would not identify these trends.

The invertebrate fauna of the Limpopo Province Northern Mistbelt Forests is largely unknown. Although invertebrates have been collected from the area, there have been no comprehensive invertebrate surveys performed, so much of the data collected during this study were new and unique, and will provide a foundation for further research. The potential for new species discoveries during this study was great and it was important to investigate distributions and endemism for each forest patch. These analyses would not be possible using morphospecies. Formal species identification based on ‘stable, interpretable and well-understood taxonomy’ was necessary to supply a solid basis for other studies (New 1998). Further, conservation prioritization of the forest patches could not be determined using morphospecies. According to Stork & Samways (1995), the most important information available to a nation in its attempts to preserve biodiversity is the knowledge of species identity and distribution.

Because of the uncertainty surrounding the use of morphospecies, the fundamental goals and the pioneering nature of this study, it was important to identify all possible specimens to the formal species level. The accuracy of morphospecies in the context of Limpopo Province forest invertebrates is assessed in Chapter 5.

2.1.3 Focal groups vs. target groups

Due to their hyperdiversity, it is impossible to produce definitive species lists of all invertebrates on any broad scale, surveys are rarely sufficiently funded to support such an undertaking (Oliver & Beattie 1996a) and one specialist or group of specialists cannot possibly assess the great variety of invertebrate taxa (New 1998), even of a single area. As a result, invertebrate biodiversity studies often focus on a single ‘focal group,’ a subdivision of the larger group of interest.

A focal group cannot be arbitrarily selected because not all invertebrate groups are equally informative. It is important to select a focal group with existing taxonomic knowledge and information (New 1998) since records of poorly known groups are far less informative than data for groups where species can be identified and something is known about the group’s status, ecology and habitat requirements (Kirby 1992). According to Hammond (1995), a focal group should be easily and reliably sorted and identified, adequately represented in conveniently taken, standardized samples and matching with the larger groups of interest. Further, knowledge of a focal group’s feeding habits, habitat needs and dispersal ability, for example, are also useful. A focal group should in essence provide reliable and informative data for a minimum of effort.

However, it is often difficult to identify a single representative focal group and it is more appropriate to select several subtaxa that together form a composite focal group (Hammond 1995). This multi-taxa or ‘shopping basket’ approach can help produce a more accurate and broader depiction of the larger group of interest (Oliver & Beattie 1996a; Kotze & Samways 1999b,). To improve the scope of the composite focal group, selected taxa should represent all major functional guilds and cover the full range of body sizes and dispersal abilities (Hammond 1995). A balance must be obtained where many groups are sampled within the constraints of taxonomic knowledge, availability of experts, logistical support and financing (Stork & Samways 1995).

According to New (1998), the practicalities of sampling and identification tend to prohibit all focal invertebrates in a survey from being incorporated into analysis, synthesis and decision-making. Therefore, various focal groups may need to be removed from the data

to be processed, effectively re-focusing the inventory. For the purpose of the present study, the remaining focal groups used in analysis are called ‘target groups.’

2.1.4 Invertebrate collection techniques

Extensive quantified sampling of invertebrates is a daunting task, since it is time consuming, labour intensive and rarely considered to be cost-effective (Oliver & Beattie 1996a; Slotow & Hamer 2000). Invertebrates are diverse, abundant and are often cryptic (Noyes 1989), they vary greatly in size and behaviour, inhabit a wide variety of microhabitats (Slotow & Hamer 2000) and many are only active for short periods each year (New 1998). Any surveyor of invertebrate diversity must consider all of these factors when choosing appropriate sampling techniques.

There are many methods available for invertebrate sampling, but all can be categorized as either active or passive. Both active and passive techniques are useful, but each has its limitations.

Passive sampling relies upon the natural movements and activity of invertebrates or upon bait for capture (New 1998) and usually involves setting large numbers of a single type of trap (Slotow & Hamer 2000). Many trap types can be used, including malaise traps, flight intercept traps, pan traps, bait traps and emergence traps (New 1998). However, pitfall traps, designed to catch ground-dwelling invertebrates, are the best-known and most often used passive sampling technique. Passive sampling is frequently used in invertebrate diversity studies because it is usually cost and labour efficient (New 1998) and active species that are difficult to sample by hand or net can be easily captured. Traps can also catch species that are active during difficult or inconvenient hours (e.g. nocturnal species), species that are often hidden (Slotow & Hamer 2000) and highly mobile species that readily fly or jump away from a collector. Passive sampling is also easily replicated and allows for reliable comparative interpretation (Duelli *et al.* 1999) because there is no bias towards the collector’s abilities or preferences (New 1998).

However, there are disadvantages to passive sampling using traps. First, most trapping methods indiscriminately kill all captured specimens. Often very large, unnecessary numbers of target invertebrates are sampled and non-target groups are discarded (Slotow &

Hamer 2000). Because biodiversity inventories must avoid destructive methods (Duelli *et al.* 1999) and removal and killing of specimens should be kept at a minimum (Kirby 1992), this raises serious ethical and conservation issues (Slotow & Hamer 2000). Secondly, traps are biased towards species with specific behaviours (Hammond 1995), such as very mobile species. Less mobile species are not sampled at all (Slotow & Hamer 2000) and traps may not capture all species in a target group equally. Invertebrate groups and even species within the same taxon can display differential trapability depending upon the organism's powers of mobility, rate of movement and activity periods (Topping & Sunderland 1992; Lowman *et al.* 1996; Luff 1996). For example, Halsall and Wratten (1988) have shown that the trapability of some carabid beetle species is very low and data collected for those species using pitfalls would be inaccurate. Finally, catch size and efficiency can be influenced by incidental variables such as temperature and weather, local topography, surrounding vegetation and exposure (New 1998). These discrepancies can produce false representations of diversity.

Quantified active sampling, where animals are pursued and captured (New 1998), involves searching for specimens in a defined plot such as a quadrat or transect or for a certain period of time. Active searching is a useful technique for collecting a wide variety of invertebrates, including spiders (Coddington *et al.* 1996; Marc *et al.* 1999), beetles (Bonham *et al.* 2000), molluscs (Emberton *et al.* 1996; McCoy 1999; Tattersfield, Warui, Seddon & Kiringe 2001), millipedes (Dangerfield & Telford 1992; Bonham *et al.* 2000) and many litter macroinvertebrates (Mesibov 1998). Unlike trapping techniques, this method can sample species equally, regardless of their habits, including less mobile and cryptic species (New 1998; Slotow & Hamer 2000). Active searching allows for the extraction of species that are found only in soil, under logs and in other specific microhabitats. This method is not wasteful or destructive like trapping since the collector can select the number of individuals that are preserved for identification. Once a reference collection is created, large numbers of specimens can be collected, identified, counted and released on site.

However, there are disadvantages to quantified active sampling. Active sampling tends to be more labour-intensive than sampling with traps. Success depends largely upon the vigilance of the collector and returns may be low, particularly for species that are widely dispersed (New 1998). Collecting very mobile species, especially those that fly or jump,

can be quite challenging and individuals may be seen but not captured. Care must be taken to ensure that sampling reflects abundance, not simply activity or apparency (New 1998). Finally, methods must be carefully designed to be repeatable. All effort must be accurately quantified (Slotow & Hamer 2000), either temporally or spatially (New 1998), to allow for accurate comparison between sites.

Because of the bias associated with all sampling techniques, invertebrate diversity may be incorrectly portrayed when only one technique is used (New 1995). No single method evenly samples all habitats and most only capture a restricted component of the target species present (Hammond 1995). The use of multiple and complementary ‘sampling sets’ increases the probability of obtaining an unbiased, truly representative sample of the species present in an area (Dangerfield & Telford 1992; Slotow & Hamer 2000). Therefore, a combination of active and passive techniques was employed for this study.

2.2 STUDY SITES

There are 18 patches of indigenous Northern Mistbelt Forests in the Limpopo Province established or proclaimed as conservation areas and managed by the South African Department of Water Affairs and Forestry (DWAF). These forests range in size from 17 to 4625 hectares. Some were conserved as early as 1903 and others as recently as 1992. Included in these areas are representatives of all three Northern Mistbelt Forest subtypes.

Due to time and funding constraints, not all 18 forests could be studied. Therefore, it was necessary to examine a more limited number of forest patches, those that would provide the most accurate representation of all of the forests. Patches were chosen to reflect the range of sizes, locations, altitudes, isolation and forest subtypes present in all 18 forests. A total of 11 forests were sampled, six in the Soutpansberg and five in the northern Drakensberg. The location, size and subtype of each sampled forest are given in Table 2.1. The distribution of forests included in this study are presented in Figure 2.1.

Table 2.1: Characteristics of forest patches sampled in this study. The name, location, size, forest subtype and vegetation characteristics of each forest are given (Geldenhuys & Venter 2002; von Maltitz *et al.* 2003), with species percents calculated.

Forest Name	Location	Area (ha)	Forest Subtype	Total Number		Typical Forest		Typical Woodland	
				of Plant Species	Woody Species (%)	Tree & Shrub Species (%)	Tree & Shrub Species (%)		
Grootbosch	Drakensberg	4625	Mistbelt	122	66	97	0		
Thathe Vondo	Soutpansberg	2000	Mistbelt	166	63	88	3		
Entabeni (Matiwa)	Soutpansberg	1393	Mistbelt	141	67	93	1		
New Agatha (Mmakgowa)	Drakensberg	1255	Mistbelt & Semi-deciduous scrub	134	76	84	8		
Roodewal	Soutpansberg	612	Semi-deciduous scrub	99	83	59	42		
Hanglip	Soutpansberg	354	Mistbelt & Semi-deciduous scrub	135	68	85	7		
Baccarat	Drakensberg	309	Mistbelt	96	70	95	2		
Goedehoop	Soutpansberg	243	Mistbelt	91	64	90	2		
Ratombo	Soutpansberg	171	Semi-deciduous mixed	104	80	71	11		
Forest Glens	Drakensberg	71	Mistbelt	64	61	94	0		
Swartbos	Drakensberg	52	Mistbelt	51	67	100	0		

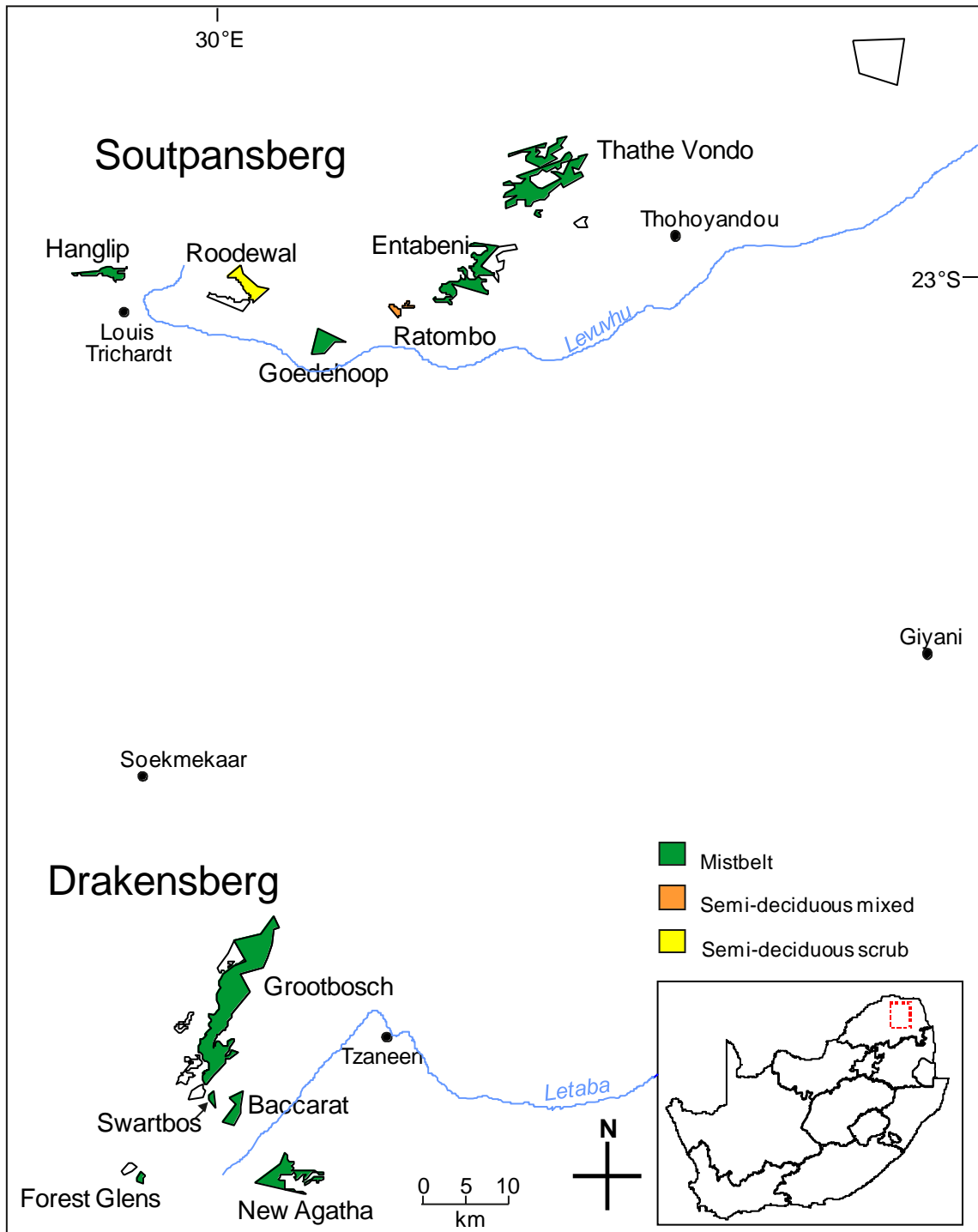


Figure 2.1: Distribution of forests studied in Limpopo Province and associated forest subtypes (modified from Geldenhuis & Venter 2002). Outlined regions are conservation areas and nature reserves managed by the Department of Water Affairs and Forestry. Study sites are indicated by shading.

The forests sampled in the Soutpansberg comprise part of DWAF's Soutpansberg Forest Management Unit and those in the Drakensberg are included in the Letaba Forest Management Unit. Because commercial farms, managed plantations or communal lands surround most of the forests sampled, they have been conserved primarily to protect natural ecosystems and water catchments. Thathe Vondo, however, is located within the former Venda Homeland and contains the Sacred Forest, which is also preserved for cultural reasons and to protect gravesites.

Because the forests of the Soutpansberg and northern Drakensberg are distributed in a linear fashion along the mountain ranges, care was taken to sample the forests in a random, non-linear order. Forests were sampled in different orders during each of the four sampling periods.

Geldenhuys & Venter (2002) completed a comprehensive survey and analysis of indigenous forest plant communities in Limpopo Province. In the 21 forests sampled, a total of 442 species in 278 genera and 100 families were identified, 308 (68%) of which are woody species.

Analysis of data for the 11 forests sampled in the present study showed that Roodewal and Ratombo have the highest percentage of woody plant species (80% or more) and a much lower percentage occurs in Thathe Vondo, Goedehoop and Forest Glens (less than 65%). A high percentage (90% or more) of typical forest trees and shrubs were identified in Grootbosch, Entabeni, Baccarat, Goedehoop, Forest Glens and Swartbos, all of which are classified as the mistbelt forest subtype. However, relatively fewer typical forest trees and shrubs were found in Roodewal (59%) and Ratombo (71%), classified as semi-deciduous scrub forest and semi-deciduous mixed forest respectively. Table 2.1 lists the vegetation characteristics of the sampled forests.

Basal area, an estimate of a forest's growing stock, was found to be between 30 and 60 square metres per hectare in the mistbelt forests studied by Geldenhuys & Venter (2002), but was only between 13 and 22 square metres per hectare in the other forest subtypes sampled. Analysis also showed that 98 plant species, primarily trees and shrubs, are endemic to the total study area, have a disjunctive presence in the total study area, are potentially new species or are at the northern or southern range limit of the species. In

addition, 19 exotic plants were identified, but none was recorded in large numbers and nowhere were they considered problematic, except in parts of Ratombo.

2.3 STUDY TAXA

Ten focal taxa were chosen from the invertebrate macrofauna of the Limpopo Province forests to be included in this study. The focal groups were selected to represent different ecological niches, microhabitat preferences, mobilities and sizes. The trapability of the groups was also considered when selecting taxa to investigate. In addition, species level identification of specimens was necessary (Section 2.1.2) so groups with available taxonomic expertise were selected.

The focal taxa chosen to be included in this study were millipedes, centipedes, scorpions, spiders, molluscs, earthworms, amphipods, selected pollinating flies, dragonflies, damselflies and butterflies. However, sampling and identification for some of these groups was not successful (see Section 2.4.4). Therefore, the target taxa were rationalized. The final target taxa selected were millipedes, centipedes, scorpions, web building and ground wandering spiders, terrestrial molluscs, earthworms and terrestrial amphipods.

2.3.1 Millipedes (Class: Diplopoda)

Millipedes are important and abundant soil arthropods (Hamer 2000) and are found throughout the world in most biomes and vegetation types, but are especially diverse in the tropics (Ruppert & Barnes 1994; Hamer & Slotow 2002). They are secretive, mostly nocturnal animals, usually found in leaf litter, under stones, bark and decomposing logs and in the soil (Hopkin & Read 1992; Hoffman 1993; Ruppert & Barnes 1994). The seasonal activity of millipedes is largely determined by temperature and moisture availability of the area (Hopkin & Read 1992).

The vast majority of millipedes are detritivores and feed upon decomposing plant material (Hopkin & Read 1992; Hoffman 1993; Ruppert & Barnes 1994). They are important components of forest ecosystems and soil nutrient cycles because they fragment dead vegetation, stimulate microbial activity and promote decomposition (Hopkin & Read 1992;

Hamer & Slotow 2002). For example, nocturnal surface feeding millipedes inoculate leaf litter with fungal spores and bacteria when returning under cover for the day (Hopkin & Read 1992). Millipedes also serve as food of a variety of vertebrates and invertebrates (Hamer & Slotow 2002).

Millipedes range in length from two to 30 centimetres and their bodies are usually circular in cross-section (Hopkin & Read 1992; Barnes 1998; Hamer 2000). They are distinguished from the other arthropods by having five to 85 paired fused segments, called ‘diplosegments,’ each with two pairs of legs except for the legless first segment (Dales 1981; Brusca & Brusca 1990; Hoffman 1993). Millipedes are also unique among all uniramians, usually having an exoskeleton reinforced with calcium carbonate (Barnes 1998). Most species possess allomone-producing glands that are arranged serially along the segments and are used to discourage predators and to inhibit fungal growth (Lawrence 1984; Hoffman 1993). Millipedes are relatively long-lived terrestrial arthropods and generally take one to two years to mature into adults, although some species may take longer (Hopkin & Read 1992). Millipedes are totally non-aggressive towards humans, as they do not bite, sting, transmit disease and rarely eat crops (Hoffman 1993). They belong to the subphylum Myriapoda, along with the Chilopoda (centipedes), Symphyla and Pauropoda (Barnes 1998).

Due to their limited powers of dispersal, millipedes exhibit a high degree of local speciation and there are a large number of endemic millipede species with restricted ranges (Hoffman 1993; Hamer 2000; Hamer & Slotow 2002). This is particularly apparent in less mobile families such as the Dalodesmidae, Odontopygidae and Gomphodesmidae (Hamer & Slotow 2002). Hoffman (1993) suggests that no other organism group has responded to the effects of isolation and fragmentation to the extent of millipedes. In addition, a range of millipede species usually occurs within any particular site, contrary to the notion that they should exclude each other through competition (Hopkin & Read 1992).

Approximately 10 000 species of millipedes have been described in the world (Brusca & Brusca 1990; Hoffman 1993; Ruppert & Barnes 1994), in 15 orders, 112 families and 1800 genera (Hamer & Slotow 2002). However, they are one of the least known larger classes of arthropods and probably only one eighth of the total millipede fauna has been described (Hoffman 1993). A large percentage of these unknown species are probably found in the

tropics, where anyone collecting can expect a large proportion of specimens to be new or rare species (Hoffman 1993).

Currently there are 552 valid species of millipedes described for southern Africa (Hamer 1998). South Africa's millipede fauna includes 484 known species in seven orders, 14 families and 61 genera (Hamer & Slotow 2002). According to Hamer and Slotow (2002), 89% of South African millipede species are endemics, 80% are regional endemics (less than 150 kilometres between any two localities), at least 500 species remain to be described and most genera require revision.

Millipedes have been recognized as informative in ecological and biodiversity studies (Hamer 2000). They are also useful in evolution and dispersal studies due to their long lineages, evolutionary stability and limited mobility (Hoffman 1993).

2.3.2 Centipedes (Class: Chilopoda)

Centipedes are carnivorous myriapods that are found throughout most of the world, in both temperate and tropical regions (Ruppert & Barnes 1994). Most centipedes are vulnerable to desiccation and predation, so they are mainly nocturnal and live in moist microhabitats such as leaf litter, soil and beneath stones, bark and logs (Lewis 1981; Ruppert & Barnes 1994). Centipedes make no elaborate nests or retreats and they do not dig burrows (Lawrence 1984). Rather, they kill and eat what they require on the spot and take retreat in any available crevice or stone (Lawrence 1984).

Most centipedes hunt at night and feed on small soft-bodied insects, worms and spiders (Lawrence 1984; Ruppert & Barnes 1994). Very large centipedes have even been known to attack lizards, frogs and small birds (Lawrence 1984). As predators, centipedes help keep the numbers of prey organisms in check.

Centipedes range in length from one to almost 30 centimetres and many are brightly coloured, especially tropical species (Hopkin & Read 1992; Barnes 1998). Centipedes are soft-bodied, elongate, dorsoventrally flattened arthropods with two pairs of maxillae and a body trunk with 15 to 181 segments (Lewis 1981; Barnes 1998). Each of these body

segments has one pair of legs, except the last two that are legless (Dales 1981; Brusca & Brusca 1990; Midgley *et al.* 1997; Barnes 1998).

About 2500 species of centipedes have been described (Lawrence 1984; Ruppert & Barnes 1994). These species fall into four principal orders and are further divided into about 20 families (Brusca & Brusca 1990; Ruppert & Barnes 1994). Currently about 150 species have been described in South Africa (Lawrence 1984). According to Lawrence (1955a), the region's centipede species are largely known, but much is still uncertain regarding their distribution patterns.

2.3.3 Scorpions (Order: Scorpionida)

Scorpions are predatory arthropods commonly found in tropical and subtropical areas of the world and the temperate regions of North America (Miller & Harley 1992). They inhabit a variety of environments on all major land masses, favouring warm areas such as deserts and tropical rain forests, but are notably absent from Antarctica (Brusca & Brusca 1990; Polis 1990; McGavin 2000). All species are terrestrial, living in all nonboreal habitats including deserts, savannas, grasslands, temperate forests, tropical forests, rain forests, the intertidal zone and mountains up to 5500 metres in altitude (Cloudsley-Thompson 1968; Polis 1990). They are nocturnal, secretive invertebrates that spend most of the daylight hours beneath logs and stones (Miller & Harley 1992). Scorpions are considered to be the most ancient terrestrial arthropods, the most primitive arachnids (Brusca & Brusca 1990; McGavin 2000) and one of the most successful and important predators in some habitats (Polis 1990).

Scorpions are the largest living arachnids with some reaching lengths of 18 centimetres, but most are much smaller (Brusca & Brusca 1990). They are relatively long-lived animals since most live for two to ten years, but some may live 25 or more years (Polis 1990).

The scorpion's diet consists mainly of spiders, harvestmen, flies, cockroaches, grasshoppers, crickets, mantids, butterflies, ants, beetles, myriapods and even small mice, snakes and lizards (Cloudsley-Thompson 1968; Polis 1990). Feeding is slow and can take several hours (Cloudsley-Thompson 1968). Scorpions are probably not active hunters, but

rather wait for prey that they locate by substrate vibrations or using pedipalpal trichobothria (Cloudsley-Thompson 1968; Polis 1990). Scorpions are able to survive well in harsh habitats such as deserts because they can live for many months without food or water (Cloudsley-Thompson 1968).

There are nine recognized families of scorpions, the largest being the Buthidae (McGavin 2000). The southern African scorpion fauna is dominated by three genera, *Hadogenes* (Ischnuridae), *Opisthophthalmus* (Scorpionidae) and *Parabuthus* (Buthidae), that together account for about 67% of the total described species (Prendini 2002).

Approximately 1400 species of scorpions have been described worldwide (McGavin 2000). The approximately 135 species described in southern Africa (Lamoral & Reynders 1975) account for 8% of the world's genera and at least 10% of the world's species (Prendini 2002). This is a high proportion compared to larger temperate regions and even some tropical regions. The southern African scorpions are well studied and 38% of the genera and at least 86% of the species are endemic to the region (Prendini 2002). There are approximately 89 scorpion species described from South Africa (Lamoral & Reynders 1975).

Scorpions are useful subjects for a wide variety of research, from biochemistry to evolutionary ecology (Polis 1990). They are valuable subjects for biogeographical research since they are a very ancient group and have limited dispersal abilities (Cloudsley-Thompson 1968).

2.3.4 Web building and ground wandering spiders (Order: Araneae)

Spiders are a large, distinct and widespread group of terrestrial insectivorous predators (Borror *et al.* 1989). They are the most familiar and best known of all chelicerates since they are one of the most abundant groups of terrestrial animals (Cloudsley-Thompson 1968; Brusca & Brusca 1990) and often come into contact with man (Leroy & Leroy 2000). Spiders have exploited nearly every terrestrial habitat, including subterranean, mountain, freshwater and intertidal environments (Brusca & Brusca 1990; Marc *et al.*

1999) and have lived successfully, virtually unchanged, for millions of years (Leroy & Leroy 2000).

Most adult spiders are solitary and spend most of their lives in the pursuit of prey (Leroy & Leroy 2000). As strict predators, spiders feed on many types of adult and immature insects, woodlice, myriapods, harvestmen, other arachnids, invertebrate eggs and even fish, lizards and birds (Cloudsley-Thompson 1968; Dippenaar-Schoeman & Jocque 1997). Some species are generalists and will eat whatever they can overpower, while others are more specialized in their diet (Leroy & Leroy 2000). As predators, spiders play an important role in maintaining ecosystems by regulating the numbers of their prey (Borror 1989). However, they also serve as prey for other animals such as toads, frogs, birds, fish, shrews, wasps and centipedes (Cloudsley-Thompson 1968; Dippenaar-Schoeman & Jocque 1997; Leroy & Leroy 2000).

35 000 to 40 000 species of spiders have been described, but this is only an estimated 30% of the existing number of spider species (Brusca & Brusca 1990; Filmer 1991; Marc *et al.* 1999). Taxonomic and biological information is also lacking and knowledge of about two-thirds of families is still rudimentary (Dippenaar-Schoeman & Jocque 1997). In the Afrotropical Region there are 71 families, some 893 genera and 5423 species identified, ranging in size from 0.48 to 60 millimetres (Dippenaar-Schoeman & Jocque 1997; Leroy & Leroy 2000).

Spiders display a staggering array of lifestyles (Brusca & Brusca 1990) that are commonly classified as three basic types: web builders, plant wanderers and ground wanderers (Dippenaar-Schoeman *et al.* 1999). Because the spider fauna is so diverse and habits and habitats so varied, only web builders and ground wanderers were selected as target groups for this study.

Because they are vulnerable to predation, most tropical web building spiders are inactive and inconspicuous during the day when most of their predators are active, constructing their webs at dusk and removing them at dawn (Dippenaar-Schoeman & Jocque 1997). Those that are diurnal tend to be very large or very tiny, construct stabilimentum into their webs to hide their silhouette or build concealed retreats (Dippenaar-Schoeman & Jocque 1997). Although most families contain web building and hunting members (Dippenaar-

Schoeman & Jocque 1997), some common web building spider families are Araneidae, Tetragnathidae, Uloboridae, Linyphiidae and Theridiidae (Leroy & Leroy 2000).

Ground wandering spiders are free-living hunting spiders that run on the soil surface when active and include those that live permanently or semi-permanently in burrows or silk-lined retreats (Dippenaar-Schoeman & Jocque 1997; Leroy & Leroy 2000). Some hunt during the day using their keen eyesight, but others rely on their sense of touch to hunt at night (Cloudsley-Thompson 1968). Most ground wandering spiders live under stones, bark or fallen logs (Cloudsley-Thompson 1968), but their habits vary widely. Spiders may dig burrows or suitable locations may be found in existing substrates. Because they are mobile and not restricted to a web, hunting spiders are less vulnerable to predation than web builders (Dippenaar-Schoeman & Jocque 1997). Spider families that comprise many ground wandering species include Theraphosidae, Lycosidae, Gnaphosidae, Zodariidae and Corinnidae (Leroy & Leroy 2000).

2.3.5 Terrestrial molluscs (Class: Gastropoda)

Molluscs are some of the best known invertebrates and most people are familiar with snails, octopus, slugs and squid (Brusca & Brusca 1990). With origins in the Palaeozoic Era (Cambrian period) 500 million years ago, molluscs are a very ancient animal group and are only exceeded by the arthropods in the exploitation of varied habitats (Runham & Hunter 1970; Pflieger & Chatfield 1988).

Unless otherwise noted, the following information was obtained from Pflieger & Chatfield (1988).

Although the majority of molluscs live in the sea, many species inhabit the land and freshwater environments. The terrestrial molluscs are largely pulmonates, gastropod species that breathe with a ‘lung’ consisting of the mantle cavity roof that is protected in a moist pocket and richly supplied with blood from a capillary network. The prosobranchs comprise another terrestrial mollusc group and they are gastropods with an operculum attached to the back of the foot that acts as a protective door when the animal withdraws into its shell.

Terrestrial snails and slugs have relatively simple life cycles, laying eggs on the ground, in the soil, in crevices, in rotting wood or in leaf litter. There is no free-living larval stage and most species reach maturity in one year, although larger species may require two to four years. There is no parental care and young are vulnerable to desiccation and predation, with only about 5% of eggs surviving to maturity. However, some individuals may survive for ten years or longer. Terrestrial molluscs vary widely in diet and comprise many feeding guilds. While most gastropods are flexible opportunists and feed on rotting vegetation, fungi, algae, lichens and green plants, others specialize on carrion, other molluscs and their eggs, earthworms or millipedes.

Terrestrial molluscs have adapted to life on land, but they are always vulnerable to desiccation and generally require a damp environment to survive. Most hide during the day under logs or stones, in leaf litter or vegetation or even underground. In addition, snails are able to retract into their shell, leaving only the mantle in the aperture unprotected. Streamlined and shellless slugs move faster than snails and prevent drying out by burying deep into the soil or into small rock or log cracks (Runham & Hunter 1970).

Terrestrial molluscs are not distributed evenly throughout the world (Solem 1984). The majority prefer chalky soils where calcium is readily available for shell construction and only slugs are largely unrestricted by calcium availability (Runham & Hunter 1970). Moist but loose soil is also beneficial for egg laying. Gastropods largely prefer warmer climates, with long periods of warm, damp weather. Terrestrial molluscs are sparsely distributed or absent from vast areas such as Antarctica, the Arctic and many deserts (Solem 1984). Local distribution is largely influenced by microclimate and the diversity of microhabitats, especially the availability of leaf litter, fallen branches, rocks, trees and herbaceous plants. For example, tropical rainforests tend to be high in species richness, but have low densities (Emberton *et al.* 1996).

There are over 75 000 recognized species of gastropods, but these are thought to represent only about half of the actual number of living species (Brusca & Brusca 1990; Barnes 1998). There are many species still to be discovered and many species collected still await names and descriptions (Brusca & Brusca 1990). Tropical terrestrial molluscs are particularly diverse, but are understudied (Brusca & Brusca 1990). Current estimates

suggest that there are between 30 000 and 35 000 species of land snails in the world (Solem 1984).

According to Herbert (1998), there are about 525 species of terrestrial molluscs that occur in South Africa and over 650 species in the southern African region. There is a high level of endemism with about 90% of the species and 15 genera endemic to the region. Terrestrial mollusc species diversity is particularly high in indigenous forests.

2.3.6 Earthworms (Class: Oligochaeta)

Earthworms are primarily soil inhabitants and are found among soil particles and leaf litter, but they also live in above ground habitats such as rotting logs, moss-covered trees trunks, animal dung and under the bark of standing trees (Lee 1985; Paoletti 1999). Most earthworms are soil burrowers (Brusca & Brusca 1990; Ruppert & Barnes 1994) and are found throughout the world in all habitats except the driest and coldest areas (Lee 1985; Ruppert & Barnes 1994). The highest numbers of earthworms are found in soils containing large amounts of organic matter or a layer of moist humus (Ruppert & Barnes 1994), while dry, sandy soils and strongly acid soils generally contain few earthworms (Paoletti 1999).

Earthworms feed upon dead organic matter, usually decaying vegetation (Ruppert & Barnes 1994). The feeding and burrowing action of earthworms is important to ecosystems because they participate in organic matter cycles and modify soil structures (Lee 1985; Sims & Gerard 1985). Earthworms release nitrogen compounds for use by plants, increase the water retaining capacity of soils, improve soil drainage and aeration, reduce erosion, promote soil mixing, affect the dispersal of microorganisms and provide channels for easy penetration of plant roots (Sims & Gerard 1985; Stork & Eggleton 1992; Edwards 2000; Groffman & Jones 2000). Because of their limited mobility, they are also useful for monitoring pollution levels, soil structural changes and agricultural practices (Paoletti 1999).

Earthworms range in length from less than one millimetre to over three metres for certain Australian species (Brusca & Brusca 1990; Lavelle 1996). They are hermaphroditic and most possess relatively complicated reproductive systems (Brusca & Brusca 1990).

Bouché (1977) classified earthworm lifestyles into three categories: (1) Epigés, which are litter dwellers, are small in body size and have uniform coloration, (2) Endogés, which construct horizontal burrows in the organo-mineral layer of the soil, are weakly pigmented and vary in size and (3) Anéciques, which burrow deeply and emerge at night to draw down organic material.

About 3500 earthworm species in 10 families are described in the world, but these species are thought to represent only half of the true number (Brusca & Brusca 1990; Ruppert & Barnes 1994; Lavelle 1996; Paoletti 1999). There are 239 indigenous earthworm species in two families known for South Africa (J. D. Plisko 2003, pers. comm.). Seven additional families and more than 40 species are also described for the country, but these are known or possible exotics (J. D. Plisko 2003, pers. comm.).

2.3.7 Terrestrial amphipods (Family: Talitridae)

Amphipods are a diverse group of mostly marine, laterally compressed and shrimp-like crustaceans found in most aquatic habitats (Ruppert & Barnes 1994; Griffiths 1999). Amphipods are usually found in great numbers and comprise a large portion of biomass in an area. They range in length from one millimetre to 25 centimetres (Brusca & Brusca 1990).

One unique family, Talitridae, has invaded terrestrial habitats (Ruppert & Barnes 1994; Griffiths 1999). Found in terrestrial, marine and freshwater environments, talitrids have colonized a broader variety of habitats and any other amphipod family (Griffiths 1999). The terrestrial talitrids, also called landhoppers, are only found in the Southern Hemisphere and the tropics (Ruppert & Barnes 1994; Griffiths 1999). They are largely nocturnal, cryptic invertebrates usually seen hopping through leaf litter (Griffiths 1999). Terrestrial amphipods are confined to moist microhabitats such as soil and humus because they are not resistant to desiccation and they have gas exchange gills (Ruppert & Barnes 1994). Terrestrial amphipods feed on angiosperm leaves and detritus (Griffiths 1999; Ruppert & Barnes 1994).

Most species of terrestrial amphipods are local endemics and this is true for the South African fauna (Griffiths 1999). There are only two genera and seven species of terrestrial amphipods in South Africa (Griffiths 1999). Only one species of terrestrial amphipod is known within the study area, *Talitriator eastwoodae* Methuen, 1913 (Griffiths 1999).

2.3.8 Additional taxa

Additional taxa, including pollinating flies (Order: Diptera), butterflies and moths (Order: Lepidoptera), plant wandering spiders (Order: Araneae), dragonflies (Order: Odonata, Suborder: Anisoptera) and damselflies (Order: Odonata, Suborder: Zygoptera) were collected during this study and many additional invertebrate groups were collected in pitfall traps. However, these data were incomplete and could not be analyzed (see Section 2.4.4). Therefore, these specimens were merely identified as far as possible and are listed in Appendix 1 and 2.

2.4 METHODS

Invertebrate sampling was carried out in 11 patches of indigenous forest managed by the Department of Water Affairs and Forestry (DWAF) in the Limpopo Province during four sampling periods. These were February/March 2001, October/November 2001, December 2001 and January 2002. Each sampling period was separated from the next by a minimum of two weeks. Sampling was carried out exclusively during the high rainfall, moist summer months when invertebrates are active.

Target invertebrates were sampled in each of the 11 forest patches using three techniques: quadrat sampling, line transect sampling and pitfall trap sampling. Quadrat and line transect sampling are active sampling techniques while pitfall trap sampling is a passive sampling technique.

2.4.1 Quadrat sampling

Ground-dwelling target invertebrates (millipedes, centipedes, scorpions, earthworms and molluscs) were collected through active searching of standard sized quadrats. Only live

individuals were sampled except for molluscs, where both live individuals and empty shells were collected. Ground wandering spiders and terrestrial amphipods, which are also ground-dwelling invertebrates, were not sampled in quadrats because they are highly mobile and could not be reliably captured by hand.

Quadrat sites were selected according to a stratified random method. Within each forest, sites were chosen to account for varying elevation, slope, soil type, soil moisture and microhabitat availability based upon a visual assessment. Because steep, slippery slopes and rocky outcrops were common in most forest patches, accessibility was a limiting factor to study site locations.

Each quadrat was two by ten metres and all quadrats were subdivided into five two by two metre plots (Figure 2.2). Each two by two metre plot within each quadrat was sampled separately to allow species accumulation curves to be drawn for each quadrat site (Appendix 3). Five quadrats were completed in each of the 11 forests, for a total of 55 quadrats for the study. Species accumulation curves were also drawn for each forest sampled (see Section 3.2, Appendix 4).

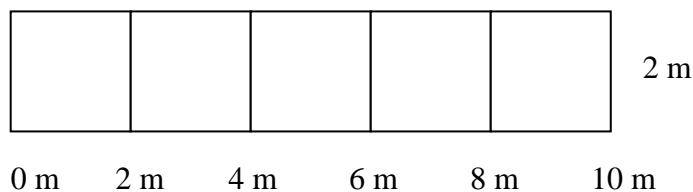


Figure 2.2: Standard quadrat size and shape for active sampling of ground-dwelling invertebrates.

Once a specific site was chosen within a forest, the quadrat search area was set up according to the Gradient Directed Transect, or Gradsect concept. A Gradsect is any transect that is purposely oriented to correspond with the perceived most significant environmental gradient in the sample area (Gillison & Brewer 1985). According to this method, sampling oriented across the greatest environmental gradient should account for the maximum number of species in an area (Wessels *et al.* 1998). Although this method is usually used for longer-distance transects, it was used in this case with respect to the gradient of microhabitats. The rectangular quadrat was oriented up the slope and situated to

encompass as many different microhabitats as possible. These microhabitats included various sized trees, rocks and logs and different leaf litter depths.

Each quadrat area was marked out and a GPS coordinate was recorded for the location. The total time spent searching each two by two metre plot was also recorded. Sampling was always conducted between 8:00 and 17:00 when enough light was available to see the forest floor properly.

Target invertebrates were collected using the hand-to-jar technique. All leaf litter was carefully turned over, along with any logs and rocks within each plot. Using a small hand trowel, the loose layer of topsoil was also excavated. Depending upon the degree of soil compactness, the amount of topsoil searched varied in depth from one centimetre in severely compacted soils to as much as 10 centimetres in plots with very loose soil. The depth searched was noted. Invertebrates from each plot within the quadrat were placed in separate jars.

Upon completion of the total two by ten metre quadrat, each jar was emptied and individuals were sorted to morphospecies based solely on external characteristics and without the aid of keys. In most cases all individuals were kept for identification. However, in cases where more than 100 individuals of the same, distinct species were collected, only about 50 individuals were kept for identification and the remainder were counted and released on site. Releases were performed with caution and all individuals were kept when there was any uncertainty of identity. Specimens returned to the laboratory from each forest were kept separate in glass tubes, preserved in 70% ethanol and were labelled with a unique code.

The number of individuals for each potential species found in each two by two metre plot was counted and entered into a large Microsoft Excel database by group.

2.4.2 Line transect sampling

Web-building spiders were collected by active searching along 100 metre line transects. Transect locations were selected according to a stratified random method, but were limited to existing foot paths or accessible areas in the forest where walking was possible through

the undergrowth and where the slope was not extreme. Transects were oriented according to the Gradsect method (see Section 2.4.1). Five line transects were completed in each of the 11 forests, for a total of 55 line transects for the study.

While walking slowly along the transect, all web building spiders seen on trees, in branches, among rocks or in herb or grass vegetation within one metre of either side of the transect line were collected. Spiders were collected off webs using small jars and lids and each was labelled with a unique numerical code. After collecting each individual, the jar code and the distance from the starting point '0' was noted in metres. The location of the web, i.e. in a tree, grass or herbs and the canopy cover of the web location was noted.

Upon completion of the 100 metre transect, the total search time was noted. The live spiders in the labelled jars were then returned to the laboratory where they were killed and preserved in glass tubes of 70% ethanol. Each specimen retained its unique code.

Because few spiders can be accurately identified in the field, specimens must be killed and preserved (Marc *et al.* 1999). However, often many spiders of the same distinct species were present within a single line transect. In these cases, they were all assigned the same code, only two or three individuals were returned to the laboratory and the others were released on site. Releases were only performed when there was no uncertainty in morphospecies identification.

The written data were then entered into a Microsoft Excel database. Species accumulation graphs were drawn for transects searched in each forest (see Section 3.2, Appendix 5).

2.4.3 Pitfall trap sampling

Plastic and glass test tubes, all 30 millimetres in diameter and 100 millimetres in length, were used as pitfall traps. Each was half filled with a solution of three parts 70% ethanol and one part glycerol. The ethanol killed and preserved any invertebrate that fell into the trap and the glycerol prevented ethanol evaporation.

To set the traps, holes were dug into the soil with a hand trowel and each trap was placed so that the top lip was flush with the surrounding soil level. Each set of pitfall traps

consisted of five individual traps placed at two metre intervals in a linear pattern. Five sets of five traps were set in each of the 11 forests. A total of 55 trap sets (275 individual traps) were used during this study. Because road and forest accessibility was dependent upon the weather, all traps could not be collected at the exact same interval. However, all traps were collected after five to seven days.

After five to seven days, the contents of each trap set were combined and treated as one sample unit. Individual traps in the same set were combined because they were not independent from one another due to the short distance between traps (two metres). Specimens were then sorted, identified as far as possible (see Section 2.4.6) and placed in glass tubes with 70% ethanol. The number of individuals in each taxon was counted for each set of pitfall traps. All animals found in the traps were retained, identified as far as possible and ultimately were lodged in museum collections for further study. All of these data, including target and non-target groups, were entered into a Microsoft Excel database. Species accumulation graphs for ground wandering spiders collected in pitfall traps were drawn (see Section 3.2, Appendix 6).

2.4.4 Other sampling techniques

Attempts were made to use other sampling techniques during this study to collect additional proposed invertebrate focal groups. Vegetation was swept to sample plant wandering spiders, leaf litter and soil was collected to extract micromolluscs and pollinating flies, butterflies, moths, dragonflies and damselflies were collected during the line transects. In addition, any focal invertebrates seen in the forest outside of study sites were collected as ‘random samples.’ However, the number and diversity of individuals collected using these methods were insufficient, could not be quantified or could not be consistently identified to species level. Further, effective sampling of flying insects is weather dependent and many of these taxa are seasonal, with adults only flying for short periods. Therefore, comparisons between sites sampled at different times would be unreliable and these data were not included in the analysis of this study. However, all specimens collected were identified as far as possible and are included in the taxon list (Appendix 1) and the collection locations list (Appendix 2).

2.4.5 Specimen identification

Each target invertebrate was identified using methods unique to each group.

- Millipedes: Specimens with dissected out gonopods were sent to Dr. Michelle Hamer, University of Natal, Pietermaritzburg, for identification. Distribution information was obtained from Hamer (1998).
- Centipedes: Scolopendromorphs, scutigermorphs and some lithobiomorphs were sent to Dr. Michelle Hamer, University of Natal, Pietermaritzburg, for identification. The remaining lithobiomorphs were sent to Dr. Gregory Edgecombe, Australian Museum, Sydney. No specialist was available to identify the Geophilomorphs further. Distribution information was obtained from various published works including Lawrence (1955a; 1984).
- Scorpions: Only one scorpion was collected in the duration of this study. The scorpion was identified to family using Lawrence (1955b).
- Web building and ground wandering spiders: Using a Wild M50 stereo microscope, J. Horn identified most spiders to family using Dippenaar-Schoeman & Jocque (1997). All spiders were then sent to Dr. Ansie Dippenaar-Schoeman, Agricultural Research Council - Plant Protection Research Institute, Pretoria, for species identification and distribution information.
- Terrestrial molluscs: All molluscs were identified by Dr. Dai Herbert, Natal Museum, Pietermaritzburg. Distributions of the collected molluscs were determined using the Natal Museum Mollusc Database and various published species accounts.
- Earthworms: Earthworms were identified by Dr. Danuta Plisko, Natal Museum, Pietermaritzburg. The distribution of each species was determined using a variety of publications including Plisko (1997) and Pickford (1937) and from the Natal Museum Earthworm Database.
- Terrestrial amphipods: There was only one species of amphipod present within the study area, *Talitriator eastwoodae* Metheun, 1913. This was confirmed using Griffiths' (1999) description of the species.
- Non-target groups collected in pitfall traps: The many non-target invertebrates collected in pitfall traps were identified by J. Horn to the most specific level

possible. Insects were sorted to family or subfamily using Scholtz and Holm (1985). Non-target arachnids were sorted to order.

- Other non-target invertebrates: Fly families Bombyliidae, Acroceridae, Asilidae and Syrphidae were sent to Dr. David Barraclough, Natal Museum, Pietermaritzburg, for further identification. Dr. Werner Barkemeyer, Naturwissenschaftliches Museum, Flensburg, Germany, also assisted in the syrphid identification. Ants were identified by Dr. Hamish Robertson, South African Museum, Cape Town. Butterflies and moths were identified by J. Horn using Pringle *et al.* (1994) and Pinhey (1962; 1975).

All specimens were lodged in appropriate museums for further future verification and study.

CHAPTER 3

INVERTEBRATE SPECIES DIVERSITY OF LIMPOPO PROVINCE FORESTS

3.1 INTRODUCTION

Species diversity is the most fundamental unit of biodiversity and measures of species diversity are commonly used to assess communities, to identify areas where biodiversity is concentrated and to evaluate the processes that promote diversity (Bond 1989a; Miller *et al.* 1995; Burgess *et al.* 1998, Purvis & Hector 2000). All of these endeavours are of relevance to both conservation and evolutionary biology (Burgess *et al.* 1998). The primary aim of this study was to investigate the invertebrate diversity of Limpopo Province indigenous forests with emphasis on conservation and management applications. In this chapter I describe the target invertebrate species composition of Limpopo Province forests and present the basic measurements of diversity, including species richness, diversity and evenness, for the Soutpansberg and Drakensberg regions and each forest sampled. By comparing the target group richness, diversity and evenness of regions and forests, and assessing the variables that influence richness, I provide information that can be used for conservation prioritisation and management. Introduced invertebrate species, which may adversely affect indigenous fauna, are also examined in this chapter.

3.1.1 Biodiversity surrogates

Biodiversity cannot be reduced to or fully captured in a single measurement since it is a multidimensional concept and only limited components can be measured (Hunter 1999; Purvis & Hector 2000). Even the elements that can be quantified are problematic since ideal measurements are often difficult or impractical to obtain (Gaston & Spicer 1998). Therefore, surrogate measures, readily quantified correlates of the actual measures desired, are often used (Gaston & Spicer 1998).

The most common biodiversity surrogate is species diversity, particularly the measure of species richness, which tends to correlate with genetic diversity, organism diversity and ecological diversity (Gaston & Spicer 1998; Hellmann & Fowler 1999). Increasing species

diversity generally implies greater diversity of genes, higher taxa, niches and habitats. However, knowing the species diversity of a single area, group or time is essentially useless unless it can be compared to other areas, groups or times (Purvis & Hector 2000). Because species diversity surrogates are often used to compare communities, to prioritize area management and as starting points for basic research, the accuracy of such measurements is important (Hellmann & Fowler 1999). In this chapter I use measures of target group species richness, diversity and evenness as surrogates for the total invertebrate diversity of Limpopo Province forests, while recognizing that invertebrate taxa with higher mobility were not sampled and they may show different patterns of diversity (see Section 5.4.1).

3.1.2 Measuring alpha diversity

With the exception of plants and some conspicuous mammals, diversity measurement by direct census is not feasible for terrestrial species (Colwell & Coddington 1994). Therefore, estimations of species diversity must be based on sampling subsets of the community. Species diversity is commonly estimated in three ways: by recording the number of sampled species, describing their relative abundances and using an index that combines these two elements (Magurran 1988).

The number of species in a given area (alpha diversity) is called species richness. Species richness is the oldest and most fundamental concept of diversity (Heltshel & Forrester 1983). When sample sizes are equal, simple counts of species, S , can be used to compare the richness between communities. This is the most clear, practical, precise and objective estimator of richness (Heltshel & Forrester 1983; Hawksworth & Kalin-Arroyo 1995; Hellmann & Fowler 1999). However, simple species counts are dependent upon sample size or scale and consistently underestimate the true richness of communities at all sample sizes (Ludwig & Reynolds 1988; Bisby 1995; Hellmann & Fowler 1999). When sample sizes are not equal, alternative richness indices must be used that are independent of sample size and are based on the relationship between S and n , the total number of individuals observed (Ludwig & Reynolds 1988). Two well-known richness indices are the Margalef (1958) index,

$$R1 = S - 1 / \ln(n)$$

and the Menhinick (1964) index,

$$R2 = S / \sqrt{n}$$

Both of these indices assume that a functional relationship exists between S and n in the community (Ludwig & Reynolds 1988).

Richness measures are clearly appealing and avoid many of the problems encountered when using models or diversity indices (Magurran 1988). Although they are also easy to obtain and calculate, richness measures contain little ecologically important information, can mask shifts in evenness and treat all species equally despite inherent differences in trophic level, size class, taxonomy, growth form, evolutionary history or rarity (Magurran 1988; Harper & Hawksworth 1994; Hawksworth & Kalin-Arroyo 1995).

The relative abundance of different species is expressed as evenness (Bisby 1995; Hunter 1999), which is an important component of species diversity since no community consists of species of equal abundance (Magurran 1988). In most communities there are a few very common species, a slightly larger proportion with medium abundance and many species represented by only a few individuals (Magurran 1988; Bisby 1995). Evenness indices are at a maximum when all species are equally abundant and approach zero as relative abundance diverges away from evenness (Ludwig & Reynolds 1988). There are several evenness indices available for use, including those developed by Pielou (1975), Sheldon (1969) and Heip (1974) that are sensitive to species richness. In contrast, the modified Hill's ratio ($E5$) is not affected by sample size or species richness (Ludwig & Reynolds 1988).

$$E5 = \frac{(1/\lambda) - 1}{e^{H'} - 1}$$

Where λ = Simpson's index
 H' = Shannon's index

The modified Hill's ratio is also the most interpretable and least ambiguous of the evenness indices (Ludwig & Reynolds 1988).

Richness and evenness are often combined with mathematical formulas into a single measure called a diversity index (Hunter 1999). Numerous diversity indices have been developed with differing units and relative weighting of richness and evenness (Ludwig & Reynolds 1988; Magurran 1988). The first diversity index, λ , was proposed by Simpson (1949). This index varies from zero to one and gives the probability that two individuals drawn at random from a population belong to the same species. Simpson's index is a dominance measure and is heavily weighted towards the most abundant species in a sample (Magurran 1988). Shannon's index H' (Shannon & Weaver 1949), the most widely used diversity index, is a measure of the uncertainty in predicting to what species an individual chosen at random from a community will belong (Ludwig & Reynolds 1988). This is an information theory index and assumes that individuals are randomly sampled from an indefinitely large population and that all species are represented in the sample (Magurran 1988). However, the units of the Simpson's and Shannon's indices can be confusing and difficult to interpret (Ludwig & Reynolds 1988).

In order to express diversity in units of species, one of Hill's (1973) diversity numbers can be used.

$$N_0 = S$$

Where S = total number of species

$$N_1 = e^{H'}$$

Where H' = Shannon's index

$$N_2 = 1/\lambda$$

Where λ = Simpson's index

Hill's diversity numbers measure the effective number of species in a sample or the degree to which proportional abundances are distributed among the species. N_0 is the number of all species in the sample regardless of abundance, N_1 measures the number of abundant species in the sample and N_2 measures the number of very abundant species. According to Ludwig & Reynolds (1988), the series of diversity numbers presented by Hill are the easiest to interpret and are much less confusing than other indices.

However, there are disadvantages to using any diversity index. Fundamentally, no single index can incorporate both richness and evenness without loss of information (Purvis & Hector 2000) and many indices make assumptions about sampling that may be difficult to meet (Bisby 1995). Interpreting diversity indices is also difficult since a given value may result from various combinations of richness and evenness and it is impossible to determine the relative importance of each component (Ludwig & Reynolds 1988). For these reasons, richness and evenness are often presented as separate values alongside diversity indices. Presentation of parallel information can provide powerful insights into ecological change and community differences (Bisby 1995).

Because of the uncertainties and limitations associated with all measures of species diversity (Ludwig & Reynolds 1988), richness, evenness and diversity indices were all calculated and expressed separately in this study. In this chapter I use simple species counts S to measure species richness whenever possible, the modified Hill's ratio $E5$ to measure evenness and Hill's diversity number NI to express diversity.

3.1.3 Introduced species

The introduction of exotic species is a major threat to global biodiversity (Section 1.1.7). Although most colonization attempts made by non-native species fail, a certain percentage of exotics do become established in new areas (Carroll & Hoffman 2000; Primack 2000). These successful exotics may then become invasive and increase in abundance at the expense of native species (Primack 2000). However, not all successful exotics are invasive species. For example, the black fire ant *Solenopsis richteri* Forel, 1909 was introduced to the United States from South America, but remains localized in northern Alabama (Carroll & Hoffman 2000).

Major South African invasions of exotic species occurred after the establishment of the European colony at the Cape in 1652 and most have happened only since the mid 19th century (Huntley 1999). At least 789 species of naturalised exotic plants occur in South Africa, 47 of which are considered of serious concern to conservationists (Wells *et al.* 1986), and 198 plant species have been declared invasive (Henderson 2001). In contrast, mammal and other vertebrate invasions appear to have had minimal impact in South

African terrestrial environments (Huntley 1999). However, the extents of faunal invasions in South African ecosystems, including those of invertebrate exotics, have not been analysed (Macdonald *et al.* 1986).

A few South African invertebrate exotics have been studied, such as the Argentine ant *Linepithema humile* (Mayr, 1868) in Cape fynbos and forest communities, where it has displaced native ant fauna and reduced the diversity of other invertebrates (Breytenbach 1986; Ratsirarson *et al.* 2002). However, introduced invertebrates in South Africa are largely known only as pests of imported crops (Samways 1981). The numbers of exotic invertebrates that have invaded natural communities have not been identified (Breytenbach 1986).

Throughout this study, introduced invertebrate species have been distinguished from indigenous species and have been excluded from all analyses unless otherwise noted. Exotic species could be incorporated, but in terms of the measures described in this chapter, they need to be dealt with separately since they do not contribute positively to biodiversity. In this chapter I describe the composition and abundance of introduced invertebrate species in Limpopo Province forests.

3.2 METHODS

Invertebrates from the seven target taxa were sampled according to the three sampling methods in 11 forest patches in Limpopo Province as described in Chapter 2. Species accumulation curves were drawn for the species sampled in quadrats, transects and pitfall traps in each forest using two methods: (1) *Field species accumulation curves*, which were drawn according to the order in which sites were sampled and (2) *Randomised species accumulation curves*. Randomised species accumulation curves were generated with the computer program EstimateS (Colwell 1997) using 100 randomisations. The species accumulation curves are given in Appendices 4, 5 and 6. Only ground wandering spiders were included in the species accumulation for pitfall traps because other ground-dwelling target groups (millipedes, centipedes, molluscs, earthworms and scorpions) were more reliably quantified in quadrats and no additional species from these groups were sampled

in pitfalls. Amphipods were not included in pitfall accumulation curves because there was only one species.

Two different approaches were used to measure richness, diversity and evenness. The first method used mean values calculated from individual samples, which had variance and therefore allowed for statistical comparison. The second method, here called ‘absolute,’ was cumulative and considered all samples from each locality in calculations.

3.2.1 Calculations of richness, diversity and evenness

Richness, diversity and evenness were calculated for each region (i.e. Drakensberg and Soutpansberg), each forest and each target group within each forest. Simple species counts S were used to measure richness and the indices NI and $E5$ were used to measure the diversity and evenness of regions, forests and target groups within forests. All figures were calculated using the SPDIVERS.BAS program of Ludwig & Reynolds (1988).

3.2.2 Comparisons of richness, diversity and evenness

Statistical comparisons were made between the richness, diversity and evenness of regions, forests and target groups within forests. All data were analysed using the statistical software SPSS (Norusis 1994). The normality of the data distribution was determined by performing a Kolmogorov-Smirnov goodness of fit test. When necessary, data that were not normally distributed were log transformed. One way ANOVAs were used to test for significant differences between regional, forest and target group richness, diversity and evenness. The LSD post hoc test was used to identify significant differences between individual forests and target groups within each forest.

3.2.3 Absolute species richness, diversity and evenness

The absolute or cumulative measures calculated for regions, forests and target groups have no variance and could not be subjected to statistical analysis. As a result, only simple comparisons could be made between values and the integrity of all comparisons was dependent upon equality of sample sizes.

Because the Drakensberg and Soutpansberg sample sizes were not equal, $R1_{ab}$ and $R2_{ab}$ were used to calculate absolute regional species richness. However, $R1$ and $R2$ can be unreliable and can vary with sample size (Ludwig & Reynolds 1988), so an alternative absolute regional richness measure was also used. Simple species counts S_{ab} , which are more straightforward and interpretable, were calculated for each region after Hanglip was removed from the analysis to equalise sample size. Hanglip was withdrawn because it is a forest of intermediate size, its forest subtypes are represented in the region by other forests and it only contained three unique species. Individual forest sample sizes were equal, so S_{ab} was used to measure the absolute species richness of each forest and target group within each forest.

Absolute diversity NI_{ab} and evenness $E5_{ab}$ were also computed for each region, forest and each target group within each forest. All figures were calculated with the SPDIVERS.BAS program (Ludwig & Reynolds 1988).

3.2.4 Descriptive models - multiple regression analysis

Multiple regression was used to explain the patterns of total forest richness and individual target group richness in forests. Six models were generated including one for the total target group richness (S_{ab}) of forests and five for the richness (S_{ab}) of individual groups investigated (millipedes, centipedes, molluscs, earthworms and spiders). A backward stepwise multiple regression analysis was used to determine the combination of biotic and abiotic factors that best predict invertebrate species richness in Limpopo Province forests. All analyses were performed using SPSS (Norusis 1994). The variables assessed in the models are listed in Table 3.1. Annual precipitation, temperature and forest subtype were excluded from the regression analysis because these variables are strongly correlated with altitude.

Table 3.1: Biotic and abiotic variables assessed in the multiple regression analysis.

Size	Total size of forest*
Altitude	Mean altitude of forest
Isolation	Distance to the nearest forest patch of equal or greater size
Plant richness	Total number of plant species in forest*

*From Geldenhuys & Venter (2002)

Models were generated using all possible combinations of the given variables. The best models were determined based on the values of the adjusted R^2 and the numbers of significant variables.

3.2.5 Introduced species

Invertebrates were sampled from the 11 forest patches without knowledge of introduced species' identities. Each specialist (Section 2.4.6) identified introduced species and all data were subsequently separated as indigenous versus introduced species data.

A one way ANOVA was used to test if numbers of indigenous and introduced species in Limpopo Province forests were significantly different. The statistical program SPSS (Norusis 1994) was used to analyze the data and the normality of the data distribution was determined by performing a Kolmogorov-Smirnov goodness of fit test.

3.3 RESULTS

3.3.1 Total numbers of species and individuals

A total of 20 627 individual invertebrates were sampled during this study, from at least 33 orders, 125 families, 122 genera and 187 species (Appendix 1). Because many non-target individuals could not be identified to species, these numbers are certainly underestimates.

A total of 11 969 indigenous target group individuals were sampled, comprising 14 orders, 50 families, 86 genera and 142 species. Table 3.2 is a summary of the number of indigenous individuals and species sampled in each forest.

The total numbers of indigenous species identified in the present study represent between one and five percent of the total recognized South African fauna, depending upon target group (Table 3.3).

Table 3.2: Total numbers of indigenous target group families, genera, species and (individuals) sampled in Limpopo Province forests. Forest names are abbreviated as follows: Hanglip = HAN, Roodewal = ROD, Goedehoop = GHP, Ratombo = RAT, Entabeni = ENT, Thathe Vondo = TV, Grootbosch = GRO, New Agatha = NAG, Swartbos = SWB, Baccarat = BAC, Forest Glens = FGL. Taxa that could not be identified beyond order are indicated by (*).

Group	Order	Number of species (individuals) in each forest													
		SOUTPANSBERG						DRAKENSBERG							
		Total Families	Total Genera	Total Species	HAN	ROD	GHP	RAT	ENT	TV	GRO	NAG	SWB	BAC	FGL
Millipedes	Polydesmida	2	2	8	1 (21)	3 (55)	2 (49)	2 (33)	2 (43)	1 (94)	3 (135)	2 (32)	2 (68)	4 (77)	2 (111)
	Spirotraptida	2	5	8	1 (63)		3 (134)	4 (31)	1 (164)	1 (316)	2 (113)	3 (127)	2 (17)	3 (20)	1 (1)
	Spirobolida	1	1	2		1 (444)	1 (2)		1 (1)	1 (1)					
	Sphaerotheriida	1	1	6	4 (36)	4 (223)	3 (46)	2 (35)	2 (50)	2 (16)	2 (40)	4 (209)	2 (13)	4 (175)	3 (370)
Centipedes	Lithobiomorpha	1	2	2	1 (106)	1 (2)	1 (111)	2 (51)	1 (63)	1 (57)	1 (242)	1 (487)	1 (290)	2 (183)	1 (466)
	Scolopendromorpha	1	2	4	1 (2)	1 (22)			1 (1)		2 (41)	3 (84)	1 (18)	2 (29)	1 (7)
	Geophilomorpha*				(111)	(45)	(39)	(22)	(44)	(138)	(179)	(87)	(97)	(9)	(143)
	Scutiggeromorpha	1	1	1		1 (28)	1 (1)	1 (8)			1 (4)	1 (23)	1 (4)	1 (1)	1 (2)
Molluscs	Eupulmonata	11	14	33	15 (288)	12 (244)	7 (49)	9 (73)	15 (183)	13 (226)	11 (39)	13 (109)	8 (32)	9 (34)	15 (752)
	Sorbeoconcha	1	1	1		1 (2)	1 (2)					1 (2)		1 (1)	
Earthworms	Haplotaaxida	2	2	5	1 (60)	1 (4)	2 (30)	1 (29)	2 (98)	1 (952)	2 (656)	2 (65)	2 (170)	1 (257)	1 (33)
Scorpions	Scorpiones	1	1	1		1 (1)									
Spiders	Araneae	25	53	70	14 (50)	19 (42)	14 (83)	19 (68)	16 (98)	12 (47)	12 (56)	10 (14)	13 (53)	11 (35)	8 (150)
Amphipods	Amphipoda	1	1	1	1 (28)		1 (66)		1 (48)	1 (12)	1 (9)	1 (22)	1 (48)	1 (31)	1 (6)
TOTAL	14	50	86	142	39	45	36	40	50	33	37	41	33	39	34
					(765)	(1112)	(612)	(350)	(793)	(1859)	(1514)	(1261)	(810)	(852)	(2041)

Table 3.3: Percentage of the total number of recognized South African (SA) species and families represented in this study. Introduced species, new species and species that could not be identified are excluded.

	<i>Number of species in SA</i>	<i>Represented in this study (%)</i>	<i>Number of families in SA</i>	<i>Represented in this study (%)</i>	<i>Reference</i>
Millipedes	± 484	2.89	14	42.86	Hamer & Slotow 2002
Centipedes	± 150	4.00	8	37.50	Lawrence 1955a; 1984
Terrestrial Molluscs	± 525	4.57	26	46.15	Herbert 1998; D. G. Herbert 2002 pers.comm.
Earthworms	± 239	1.67	2	100.00	J.D. Plisko 2003, pers. comm.
Spiders	± 2900	1.03	62	40.32	Dippenaar-Schoeman & Jocque 1997

The number of individuals sampled from each group varied. Millipedes were the most sampled target group, comprising 28% of the total number of indigenous target group individuals sampled, while scorpions accounted for less than 0.01%. Figure 3.1 is a summary of the sampling frequency of target groups.

The numbers of species were not evenly distributed among the target groups. Although only accounting for 6% of the indigenous target individuals sampled, the spider group contains the most species (70). In contrast, centipedes account for 27% of indigenous target individuals sampled, but only contains seven species. Figure 3.2 is a summary of the species distribution among the target groups.

The field species accumulation curves for each sampling method (Appendices 4, 5 and 6) indicate that target group species sampled in quadrats and web building spider species collected in transects were sampled completely, as all graphs reach the asymptote. The asymptote was not reached on the field species accumulation curves for ground wandering spiders in Roodewal, New Agatha and Swartbos. None of the randomised species accumulation curves (Appendices 4, 5 and 6) reached the asymptote, indicating that forests were not sampled completely and that more species are likely to be found with additional sampling.

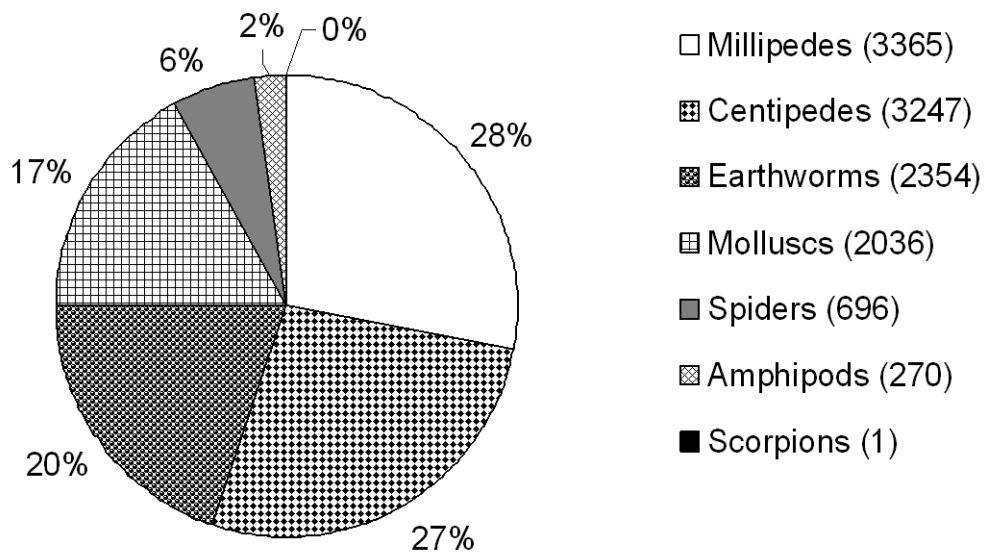


Figure 3.1: Sampling frequency of target groups in Limpopo Province forests, expressed as the percentage of the total number of indigenous target group individuals sampled (parentheses indicate the number of individuals sampled).

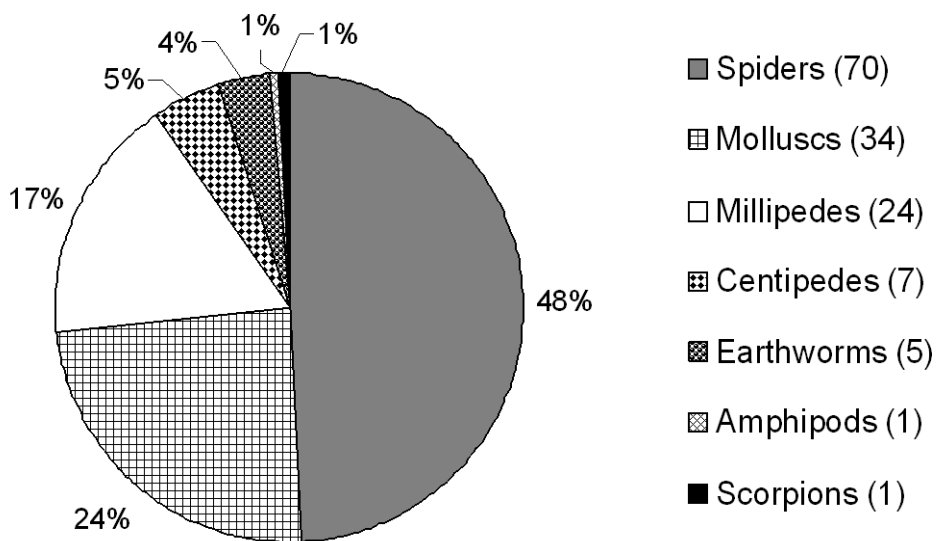


Figure 3.2: Distribution of indigenous species among the target groups in Limpopo Province forests, expressed as the proportion of the total number of species in each target group (parentheses indicate the number of species).

3.3.2 Regional comparisons of richness, diversity and evenness

There were no significant differences between regional (Soutpansberg vs. Drakensberg) richness S ($F_{1,10} = 0.015$, $P = 0.904$), diversity NI ($F_{1,10} = 1.385$, $P = 0.270$) and evenness $E5$ ($F_{1,10} = 0.994$, $P = 0.345$, Figure 3.3). In all cases the assumptions of the ANOVA were met (Kolmogorov-Smirnov test $P > 0.05$).

3.3.3 Comparisons of forest richness, diversity and evenness

There was a significant difference between the richness ($F_{10,54} = 2.557$, $P = 0.016$) and diversity ($F_{10,54} = 2.587$, $P = 0.015$) of the forests sampled, but the differences in forest evenness were not significant ($F_{10,54} = 1.548$, $P = 0.155$, Figure 3.4). In all cases the assumptions of the ANOVA were met (Kolmogorov-Smirnov test $P > 0.05$). Post hoc tests were used to determine the significance of differences between individual forests' richness and diversity (Table 3.4).

Forest Glens, Entabeni and New Agatha had the highest overall richness and Roodewal and Ratombo had the lowest. The highest diversity was measured in Forest Glens, Entabeni and Hanglip while Roodewal, Thathe Vondo and Grootbosch had the lowest. Goedehoop, Forest Glens and Ratombo had the highest evenness and the lowest was recorded in Thathe Vondo, Grootbosch and Roodewal.

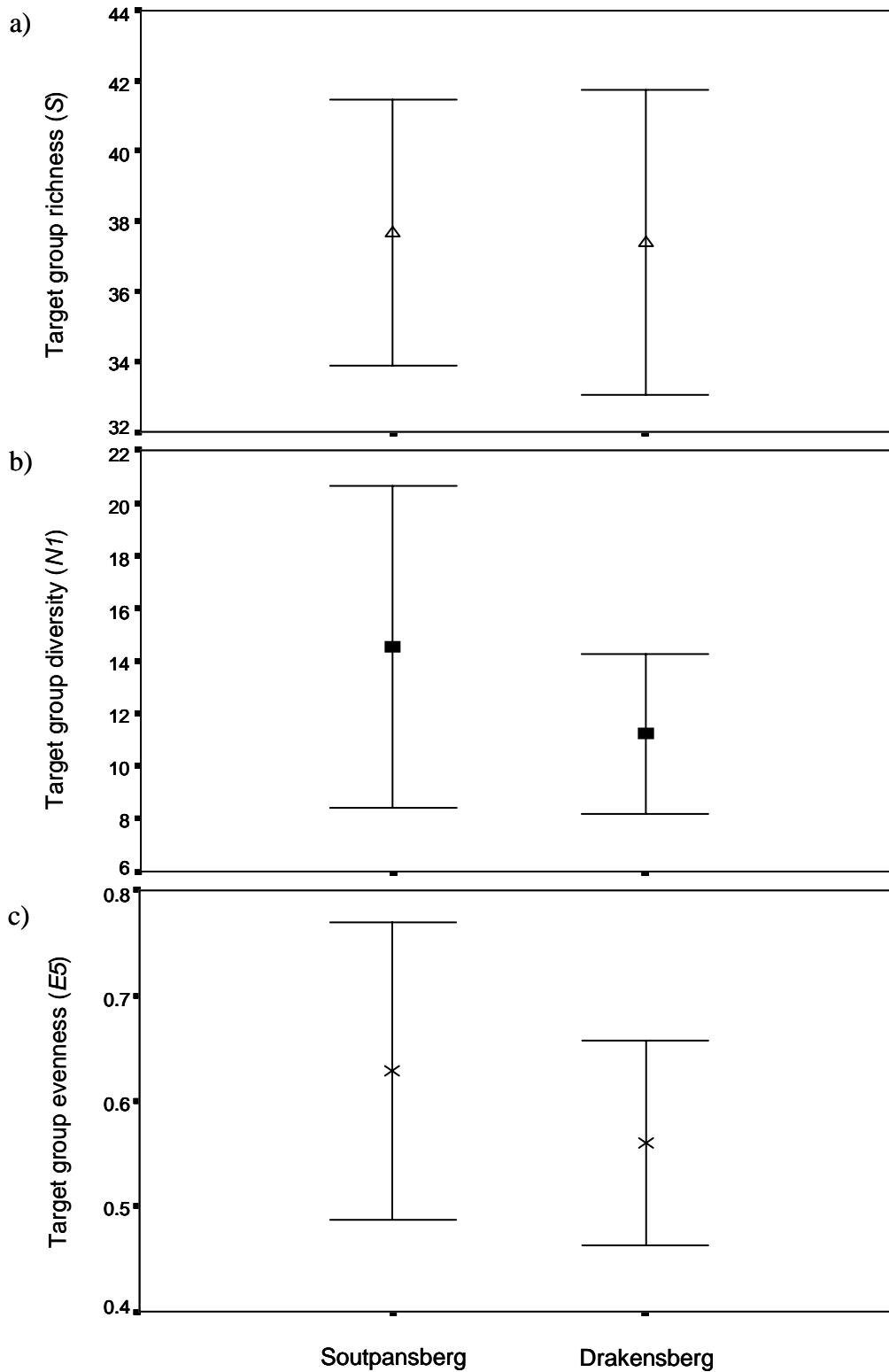


Figure 3.3: Target group a) richness S , b) diversity NI and c) evenness $E5$ of the Soutpansberg and Drakensberg regions and 95% confidence limits.

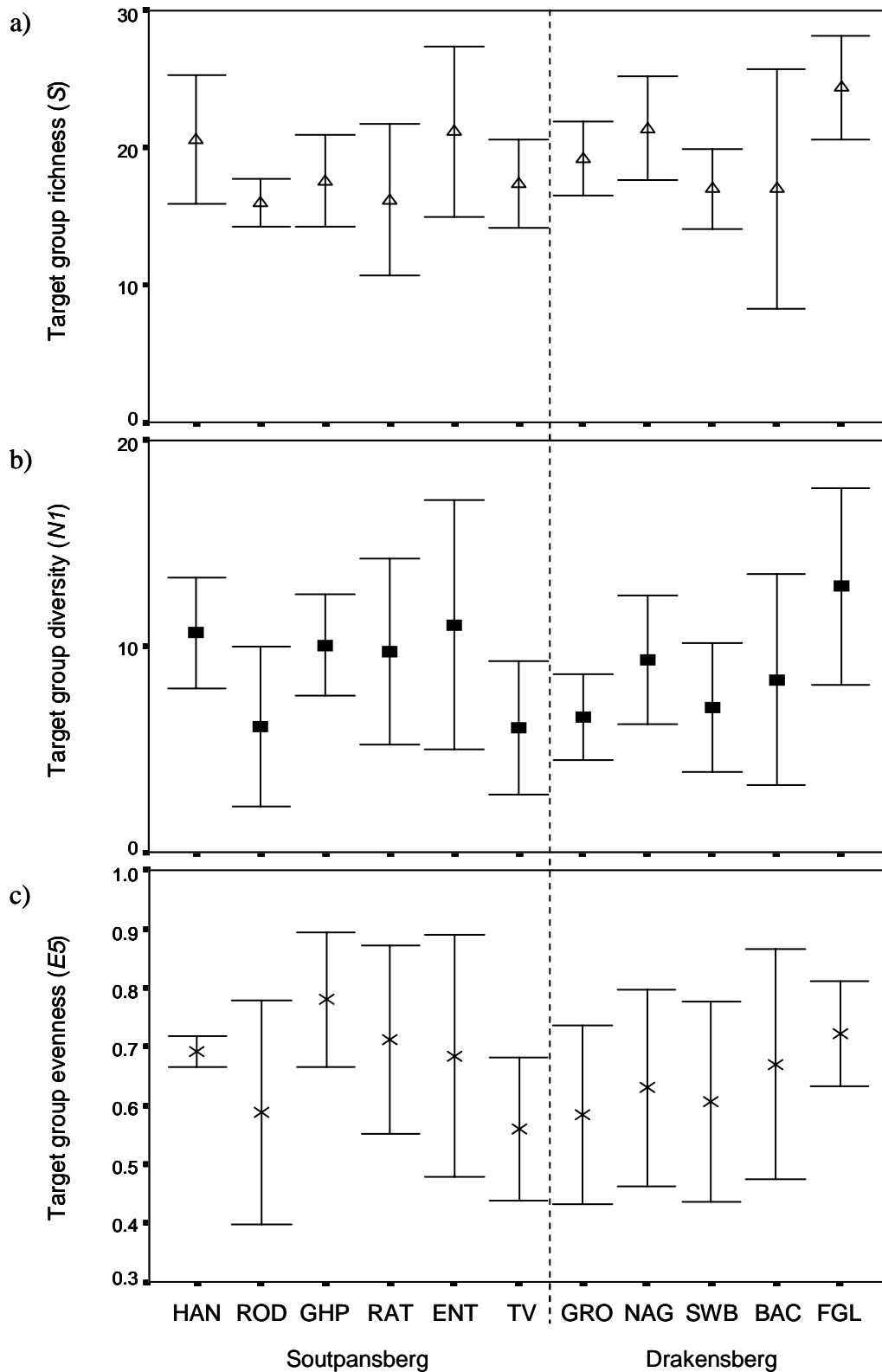


Figure 3.4: Target group a) richness S , b) diversity $N1$ and c) evenness $E5$ for each of the 11 forests sampled and 95% confidence limits. Forest names are abbreviated as follows: Hanglip = HAN, Roodewal = ROD, Goedehoop = GHP, Ratombo = RAT, Entabeni = ENT, Thathe Vondo = TV, Grootbosch = GRO, New Agatha = NAG, Swartbos = SWB, Baccarat = BAC, Forest Glens = FGL.

Table 3.4: Significant differences in richness (▲) and diversity (■) between forests, where $P < 0.05$ (post hoc test LSD). Shaded symbols indicate that the forest in the left column was higher and unshaded symbols indicate that the forest in the top row was higher. Forest names are abbreviated as follows: Hanglip = HAN, Roodewal = ROD, Goedehoop = GHP, Ratombo = RAT, Entabeni = ENT, Thathe Vondo = TV, Grootbosch = GRO, New Agatha = NAG, Swartbos = SWB, Baccarat = BAC, Forest Glens = FGL.

	HAN	ROD	GHP	RAT	ENT	TV	GRO	NAG	SWB	BAC	FGL
HAN											
ROD	□										
GHP											
RAT											
ENT		▲■		▲							
TV	□				□						
GRO	□				□						
NAG		▲		▲							
SWB											
BAC											
FGL		▲■	▲	▲		▲■	▲■		▲■	▲■	

3.3.4 Comparisons of target group richness, diversity and evenness

There was no significant difference in millipede richness ($F_{10,54} = 1.910$, $P = 0.069$), millipede evenness ($F_{10,54} = 1.856$, $P = 0.079$) and centipede diversity ($F_{10,54} = 1.783$, $P = 0.092$) between forests. However, there was a significant difference between the millipede diversity ($F_{10,54} = 2.524$, $P = 0.017$), mollusc richness ($F_{10,54} = 6.425$, $P = 0.000$), mollusc diversity ($F_{10,54} = 3.512$, $P = 0.002$), mollusc evenness ($F_{10,54} = 2.160$, $P = 0.040$), web building spider richness ($F_{10,54} = 3.315$, $P = 0.003$) and web building spider diversity ($F_{10,54} = 2.286$, $P = 0.029$) of forests. All values of target group richness (S), diversity (NI) and evenness ($E5$) calculated for forests are given in Appendix 7. Richness values for each target group in each forest are also shown in Figures 3.5 and 3.6. In all cases the assumptions of the ANOVA were met (Kolmogorov-Smirnov test $P > 0.05$).

In each sample there were few species of centipedes (average 2.87 species per sample), earthworms (average 0.80 species per sample), web building spiders (average 2.96 species per sample), ground wandering spiders (average 1.09 species per sample) and amphipods (average 0.71 species per sample). In these cases evenness is not meaningful and was not calculated. For the same reason, statistical analysis could not be performed for centipede richness, earthworm richness and diversity, ground wandering spider richness and diversity and amphipod richness and diversity.

Post hoc tests revealed the significance of differences in target group richness, diversity and evenness between individual forests. These results are given in Table 3.5.

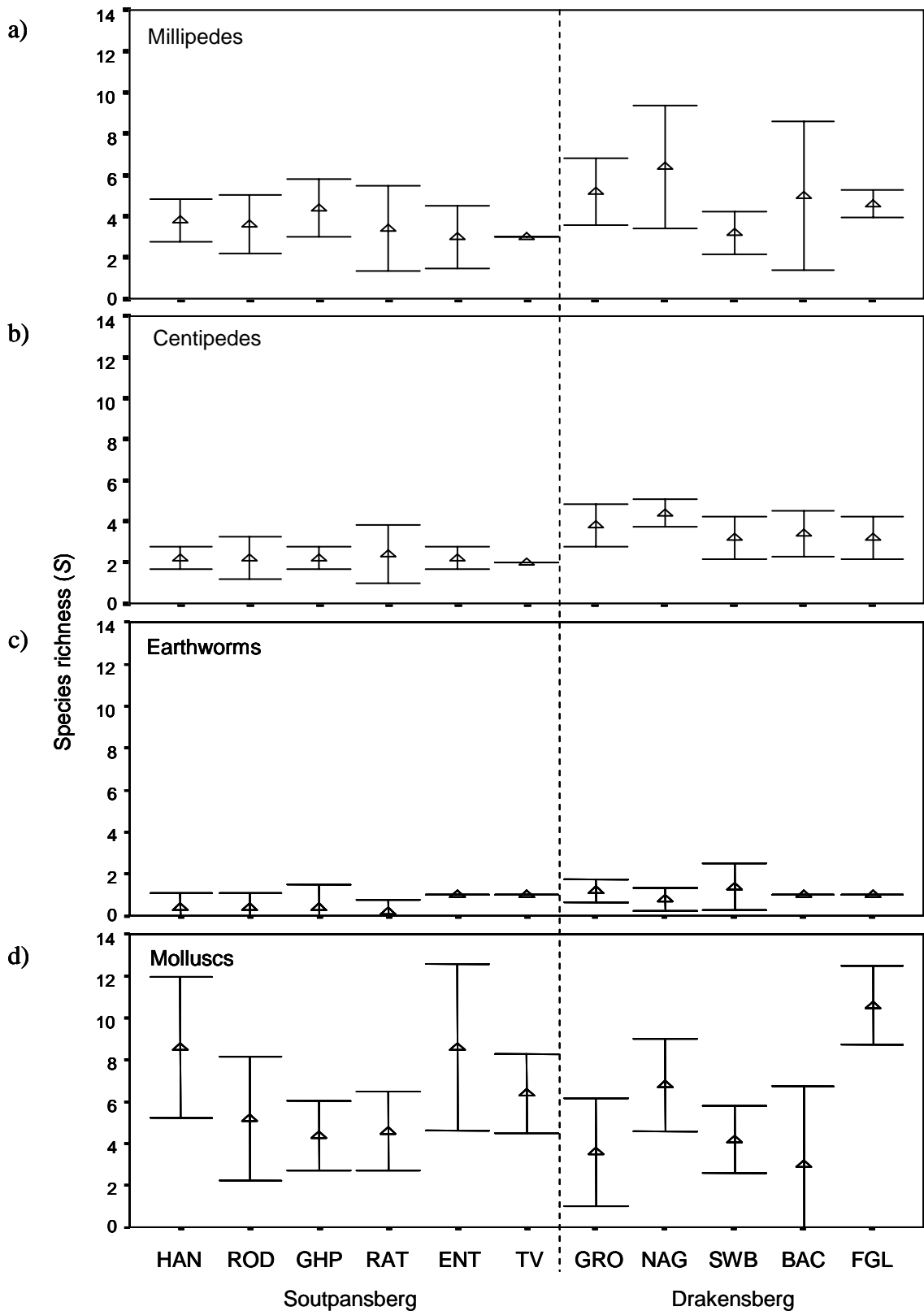


Figure 3.5: Richness (S) of a) millipedes, b) centipedes, c) earthworms and d) molluscs in each forest sampled and 95% confidence limits. Forest names are abbreviated as follows: Hanglip = HAN, Roodewal = ROD, Goedehoop = GHP, Ratombo = RAT, Entabeni = ENT, Thathe Vondo = TV, Grootbosch = GRO, New Agatha = NAG, Swartbos = SWB, Baccarat = BAC, Forest Glens = FGL.

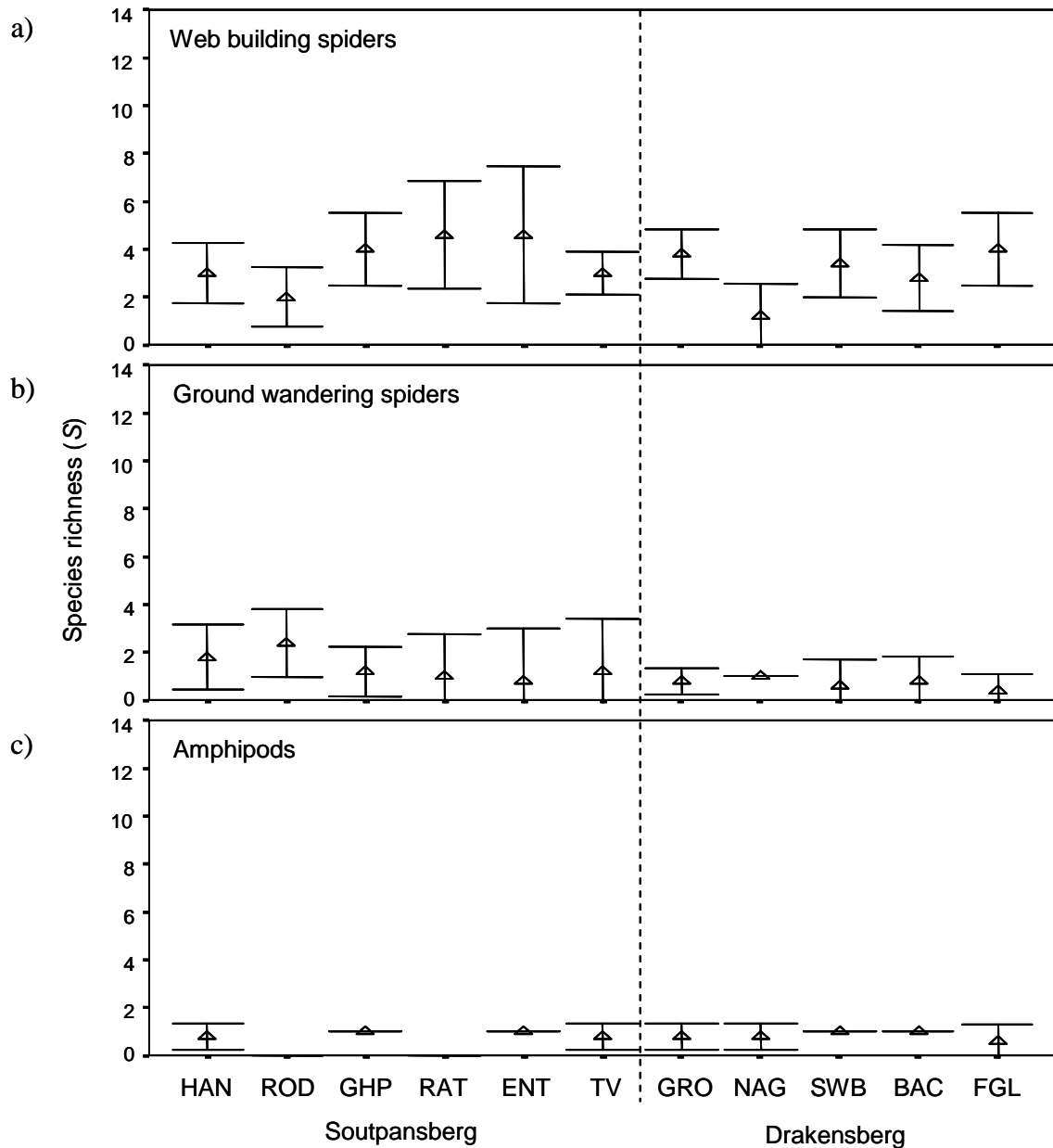


Figure 3.6: Richness (S) of a) web building spiders, b) ground wandering spiders and c) amphipods in each forest sampled and 95% confidence limits. Forests lacking symbols indicates absence. Forest names are abbreviated as follows: Hanglip = HAN, Roodewal = ROD, Goedehoop = GHP, Ratombo = RAT, Entabeni = ENT, Thathe Vondo = TV, Grootbosch = GRO, New Agatha = NAG, Swartbos = SWB, Baccarat = BAC, Forest Glens = FGL.

Table 3.5: Significant differences in richness (▲), diversity (■) and evenness (●) between forests for a) millipedes, b) molluscs and c) web building spiders, where $P < 0.05$ (post hoc test LSD). Shaded symbols indicate that the forest in the left column was higher and unshaded symbols indicate that the forest in the top row was higher. Forest names are abbreviated as follows: Hanglip = HAN, Roodewal = ROD, Goedehoop = GHP, Ratombo = RAT, Entabeni = ENT, Thathe Vondo = TV, Grootbosch = GRO, New Agatha = NAG, Swartbos = SWB, Baccarat = BAC, Forest Glens = FGL.

a)

	HAN	ROD	GHP	RAT	ENT	TV	GRO	NAG	SWB	BAC	FGL
HAN											
ROD											
GHP											
RAT											
ENT											
TV											
GRO											
NAG	■	■		■	■	■					
SWB								□			
BAC	■	■		■	■	■			■		
FGL								□		□	

b)

	HAN	ROD	GHP	RAT	ENT	TV	GRO	NAG	SWB	BAC	FGL
HAN											
ROD	△ ●										
GHP	△ ●										
RAT	△										
ENT		▲ ■	▲ ■	▲ ■							
TV											
GRO	△ □				△ □	△					
NAG		■					▲ ■				
SWB	△ ●				△ □ ●	●		●			
BAC	△ □ ●				△ □	△		△ □			
FGL		▲ ■ ○	▲ ■ ○	▲ ■		▲ ■	▲ ■	▲	▲ ■ ○	▲ ■ ○	

c)

	HAN	ROD	GHP	RAT	ENT	TV	GRO	NAG	SWB	BAC	FGL
HAN											
ROD											
GHP		▲									
RAT		▲ ■									
ENT		▲ ■									
TV											
GRO		▲ ■									
NAG	△ □		△ □	△ □	△ □	△ □	△ □				
SWB								▲ ■			
BAC				△	△			■			
FGL		▲						▲			

3.3.5 Absolute species richness, diversity and evenness

Tables 3.6 and 3.7 list the absolute species richness, diversity and evenness values calculated for each region, forest and major target group within each forest.

Table 3.6: Absolute species richness ($R1_{ab}$, $R2_{ab}$ and S_{ab}), diversity (NI_{ab}) and evenness ($E5_{ab}$) for the two sampled regions.

	Soutpansberg	Drakensberg
Richness $R1_{ab}$	12.19	9.42
Richness $R2_{ab}$	1.43	1.12
Richness S_{ab}	99	81
Diversity	25.62	25.47
Evenness	0.54	0.67

Absolute richness, $R1_{ab}$, $R2_{ab}$ and S_{ab} , and diversity were higher in the Soutpansberg than in the Drakensberg but absolute evenness was higher in the Drakensberg. Absolute richness was greatest in Entabeni and New Agatha and absolute diversity and evenness were highest in Ratombo. The lowest values were measured in Swartbos (richness), Thathe Vondo (richness and diversity) and New Agatha (evenness).

3.3.6 Descriptive models - multiple regression analysis

Multiple regression was used to determine the biotic and abiotic variables that influenced target group species richness in Limpopo Province forests. However, no significant models were found and no variables significantly affected total target group species richness. Likewise, no significant models or significant variables were detected for millipede, centipede, mollusc or earthworm species richness in forests. The only significant model generated was for spider species richness in forests.

The model that best explained the species richness of spiders in Limpopo Province forests included only one variable (Linear regression: $R = 0.654$, $R^2 = 0.427$, Adjusted $R^2 = 0.427$, $F_{1,10} = 6.714$, $P < 0.05$). The variable that significantly negatively affected spider richness in Limpopo Province forest was altitude (Linear regression: Beta = -0.651, $t_{(10)} = -2.591$, $P < 0.05$). As altitude increased, spider species richness decreased.

Table 3.7: Absolute species richness (S_{ab}), diversity (NI_{ab}) and evenness ($E5_{ab}$) for each sampled forest and major target group. Spider calculations include both web building and ground wandering spiders. Forest names are abbreviated as follows: Hanglip = HAN, Roodeval = ROD, Goedehoop = GHP, Ratombo = RAT, Entabeni = ENT, Thathe Vondo = TV, Grootbosch = GRO, New Agatha = NAG, Swartbos = SWB, Baccarat = BAC, Forest Glens = FGL.

	Soutpansberg						Drakensberg					
	HAN	ROD	GHP	RAT	ENT	TV	GRO	NAG	SWB	BAC	FGL	
Total richness	38	41	34	38	42	33	38	42	33	39	35	
diversity	16.28	9.51	15.32	21.04	19.31	5.76	9.72	11.23	8.6	11.44	15.1	
evenness	0.73	0.47	0.65	0.81	0.63	0.48	0.63	0.45	0.55	0.53	0.64	
Millipede richness	6	8	8	6	6	5	7	9	5	11	6	
diversity	3.65	3.34	4.87	4.94	3.18	2.02	4.49	5.61	3.67	7.89	3.57	
evenness	0.73	0.58	0.63	0.92	0.59	0.66	0.77	0.8	0.74	0.89	0.72	
Centipede richness	3	4	3	4	3	2	5	6	4	6	4	
diversity	2.09	3.1	1.84	3.63	2.06	1.83	2.68	2.45	2.15	1.91	1.86	
evenness	0.96	0.91	0.78	0.95	0.94	0.86	0.81	0.58	0.68	0.51	0.71	
Mollusc richness	15	12	8	9	15	12	11	14	8	10	15	
diversity	7.2	4.41	6.54	6.25	10.94	4.68	8.1	11.05	6.08	7.05	8.44	
evenness	0.73	0.59	0.99	0.84	0.85	0.53	0.97	0.9	1.02	0.85	0.73	
Earthworm richness	1	1	2	1	2	1	2	2	2	1	1	
diversity	1	1	1.84	1	1.51	1	1.9	1.36	1.12	1	1	
evenness	none	none	0.91	none	0.65	none	0.91	0.57	0.41	none	none	
Spider richness	12	15	12	18	15	12	12	10	13	10	8	
diversity	6.39	7.83	5	6.65	6.05	4.85	5.99	8.53	5.49	5.82	3.6	
evenness	0.7	0.62	0.61	0.4	0.56	0.49	0.65	1.59	0.6	0.74	0.68	

3.3.7 Introduced species

A total of 14 introduced species were sampled in Limpopo Province forests, including two mollusc species and 12 earthworm species. Introduced species were not found equally in forests and the highest number of introduced species (six) was sampled in Grootbosch, while Goedehoop, Thathe Vondo and Forest Glens only had one introduced species (Figure 3.7).

Introduced mollusc species only accounted for about 5% of all mollusc species sampled in Limpopo Province forests. In contrast, introduced earthworms accounted for the majority of all earthworm species.

Although five introduced earthworm species were found in Grootbosch, this forest also had relatively high numbers of indigenous earthworm species. When compared to numbers of indigenous species, Hanglip, Roodewal and Ratombo had proportionately more introduced earthworm species than any other forests sampled (Figure 3.8a). In terms of abundance, Ratombo had a higher proportion of introduced earthworm individuals than any other forest (Figure 3.8b).

A one way ANOVA was used to identify significant differences between data. In all cases the assumptions of the ANOVA were met (Kolmogorov-Smirnov test $P > 0.05$). There were significantly more introduced earthworm species than indigenous species sampled in Limpopo Province forests ($F_{1,21} = 6.729$, $P = 0.017$, Figure 3.9).

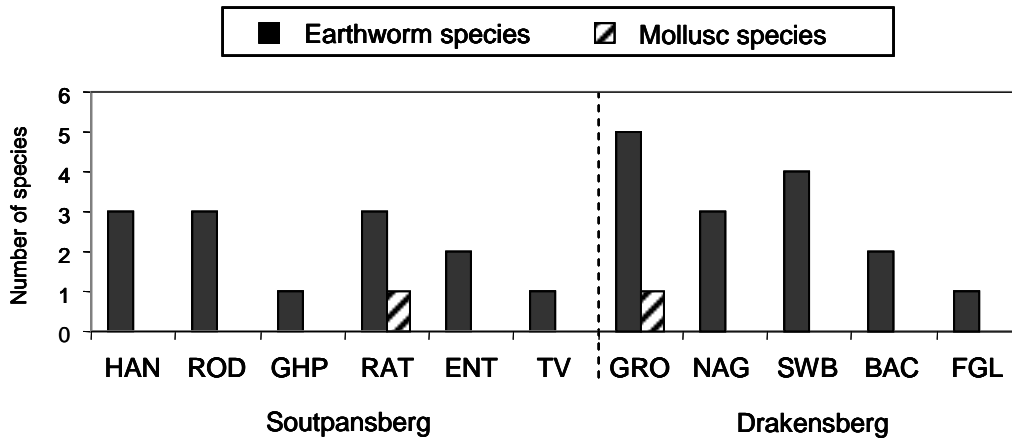


Figure 3.7: The number of introduced earthworm and mollusc species recorded in each forest. Forest names are abbreviated as follows: Hanglip = HAN, Roodewal = ROD, Goedehoop = GHP, Ratombo = RAT, Entabeni = ENT, Thathe Vondo = TV, Grootbosch = GRO, New Agatha = NAG, Swartbos = SWB, Baccarat = BAC, Forest Glens = FGL.

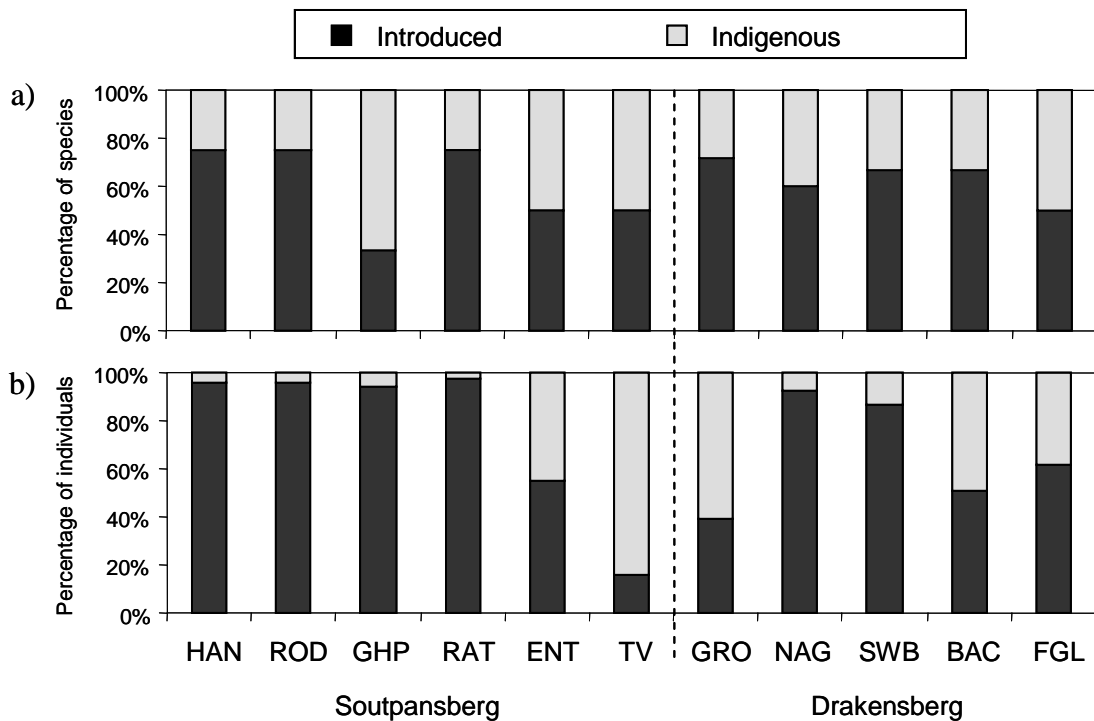


Figure 3.8: The proportion of introduced earthworms in forests for a) the total number of earthworm species and b) the total number of earthworm individuals. Forest names are abbreviated as follows: Hanglip = HAN, Roodewal = ROD, Goedehoop = GHP, Ratombo = RAT, Entabeni = ENT, Thathe Vondo = TV, Grootbosch = GRO, New Agatha = NAG, Swartbos = SWB, Baccarat = BAC, Forest Glens = FGL.

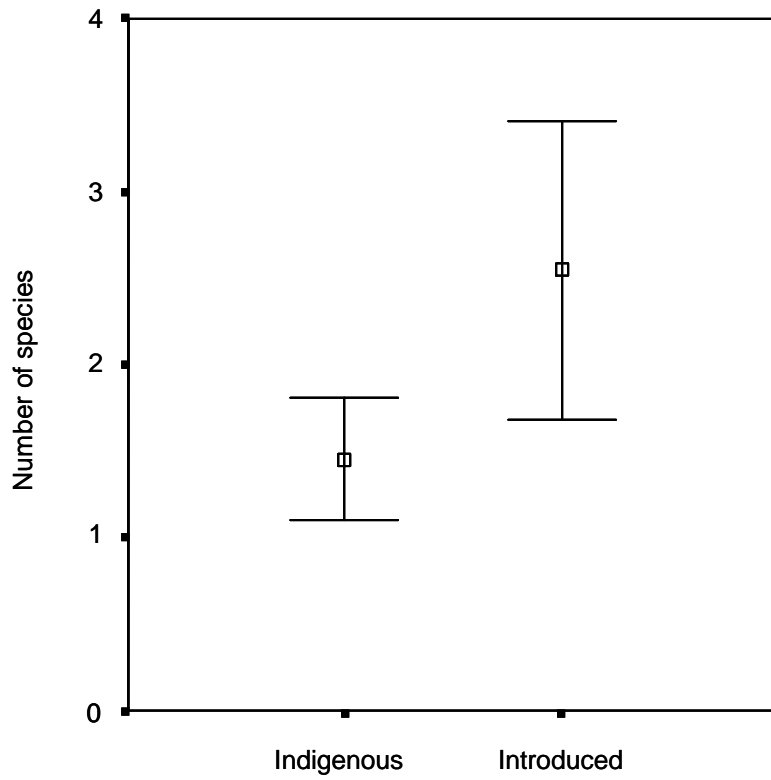


Figure 3.9: The numbers of indigenous and introduced earthworm species in Limpopo Province forests and 95% confidence limits.

3.4 DISCUSSION

3.4.1 Species composition

Despite the large number of individuals sampled during this study, it cannot be assumed that all species were represented. Although the field species accumulation curves for quadrats show that target group species were sampled completely, the randomised species accumulation curves indicate that additional target species may be found with more quadrat sampling (Appendix 4). The species most likely to be captured using this method were probably sampled, but more mobile or dispersed species may have been missed in this study.

A literature and database search (Hamer 1998; Natal Museum Mollusc Database) for millipede and mollusc localities revealed that nine species of millipedes and 18 species of molluscs were previously recorded from the study area but were not sampled during the present study. The majority of the 18 mollusc species not sampled are tiny (less than five millimetres) and cannot be sampled with active searching (D. G. Herbert 2002, pers. comm.).

The web building spider field accumulation curves indicate that it is likely that all web building spiders were collected (Appendix 5). However, the randomised species accumulation curves suggest that sampling was not sufficient (Appendix 5). Many spider species construct webs at dusk and remove them at dawn (Dippenaar-Schoeman & Jocque 1997). Because night sampling was impossible in this study, nocturnal species may not be represented and samples may only include some conspicuous, diurnal web building species. According to the species accumulation curves, ground wandering spiders were certainly underrepresented, especially in Roodewal, New Agatha and Swartbos (Appendix 6). Therefore, pitfall trapping should be more extensive and additional sampling techniques such as active searching should be used to sample ground wandering spiders more completely. The single amphipod species was successfully captured in pitfall traps, since their presence in traps mirrors that seen while searching quadrats.

Although all target group species may not have been sampled in this study, the 142 indigenous species do represent many invertebrate families and functional roles (Table 3.2).

It was not surprising that spiders were the most speciose group sampled in Limpopo Province forests (Figure 3.2), since spiders are known for high species richness (Preston-Mafham & Preston-Mafham 1984; Brusca & Brusca 1990; Marc *et al.* 1999) and comprise at least five times more species in South Africa than any other sampled taxon (Table 3.3). However, spiders were perhaps the most undersampled taxon included in this study, since I did not attempt to sample all spiders (plant wanderers were excluded) and ground wandering spiders were likely underrepresented (Appendix 6). Also striking was the lack of scorpion individuals and species encountered, since scorpions are well known inhabitants of temperate and tropical forests and three to six species occur in most locations (Polis 1990).

Millipedes were clearly the most sampled group (Figure 3.1), with up to 407 individuals of the same species encountered in a single quadrat. Centipedes were also found in large numbers, with up to 207 individuals of the same species sampled in a single quadrat. Such aggregations accounted for the large numbers of millipede and centipede individuals sampled in this study. However, these groups were relatively species poor (Figure 3.2). In order to support such high abundance, Limpopo Province forests must contain habitats favourable to millipedes and centipedes. These forests are generally moist, have thick layers of leaf litter and many dead and decaying logs on the forest floor and contain large numbers of potential prey, all of which would promote high numbers of millipedes and centipedes (see Sections 2.3.1 and 2.3.2).

3.4.2 Regional richness, diversity and evenness

Richness, diversity and evenness of the Soutpansberg and Drakensberg regions were quite similar and there were no significant differences between regional *S*, *NI* or *E5* (Figure 3.3). Absolute figures for the two regions were also comparable, although all absolute richness and diversity measures were higher in the Soutpansberg. However, these figures are difficult to interpret without examination of the species compositions. Although regional

richness, diversity and evenness were similar, it does not imply that the species compositions of regions are alike. Analyses that consider the identities of species are performed in Chapter 4.

3.4.3 Forest richness, diversity and evenness

Richness and diversity of the sampled taxa were not correlated with plant species richness. According to Geldenhuys and Venter (2002), Thathe Vondo is higher in plant species richness than any other forests sampled in this study, but it was not significantly more rich or diverse in invertebrate species than any other forest. However, plant species richness is more likely related to the richness of herbivores, which were not widely represented in this study, rather than the richness of the detritivores, decomposers and predators sampled.

In this study forests were sampled equally regardless of total size and it is possible that not all habitats were sampled in the larger forests. As a result, the well documented species-area relationship (Connor & McCoy 1979; He & Legendre 1996), could not be explored.

Absolute figures do not mirror the above trends of mean invertebrate richness, diversity and evenness (Table 3.7). The highest absolute numbers of species (S_{ab}) were sampled in Entabeni and New Agatha. In fact, all forests had higher S_{ab} than Forest Glens except Goedehoop, Thathe Vondo and Swartbos. Ratombo had the highest absolute diversity. However, these numbers have no variance and cannot be subjected to statistical analysis, so the significance of differences between absolute values is unknown.

The differences between S and S_{ab} and NI and NI_{ab} are due to the fact that S and NI are calculated with measurements of richness and diversity per sample, while S_{ab} and NI_{ab} are cumulative totals, count each species only once and are more biologically meaningful as a result. Although Forest Glens had significantly higher richness (S) and diversity (NI) than several other forests, the species compositions of samples were similar and S_{ab} and NI_{ab} were relatively low. In contrast, the invertebrate species comprising samples from Entabeni and New Agatha were more unique and produced a high S_{ab} . This same pattern is evident in the diversity measurement of Ratombo, where NI was not significantly higher

than other forests but NI_{ab} was the highest. Even though absolute measures are more indicative of the total species diversity in each forest, they do not provide insights into similarities or differences in species composition. In fact, all of the diversity measures presented in this chapter are inherently flawed because all species are not equal either conceptually or with respect to the extent of diversity that they represent (Hawksworth & Kalin-Arroyo 1995).

Absolute species richness measures were used to determine the variables that affect total target invertebrate richness levels in Limpopo Province forests. This type of analysis can provide valuable information for conservation. Once the variables that influence richness are identified, conservation efforts can be oriented towards the maintenance of such factors. However, none of the variables assessed significantly affected invertebrate richness in forests. This result was surprising, since at least some of the factors assessed in the model were expected to influence richness, especially forest size and isolation. Area and isolation are two of the most recognised determinants of species richness. Species numbers generally increase with increasing area and species numbers generally decline with increasing isolation (Bond 1989b). However, combinations of variables or factors not assessed in the model must influence forest invertebrate richness in Limpopo Province.

3.4.4 Target group richness, diversity and evenness

The species diversity measures for target groups within forests were expected to vary according to taxon due to their differing habits, habitat requirements and dispersal abilities. It was not surprising that richness, diversity and evenness were higher in different forests according to group (Figures 3.5 and 3.6).

Although richness (S), diversity (NI) and evenness ($E5$) values were used in this chapter to compare target group communities within forests, they are calculated independently for each community without any regard for similarities or differences in composite species. S_{ab} , NI_{ab} and $E5_{ab}$ provide better indications of the total species diversity of communities, but they also have the same fault. Therefore, all richness, diversity and evenness measures presented in this chapter are of limited value in comparing communities and for practical applications of conservation and management.

For all groups except spiders, no models or variables were identified that significantly affected species richness. Like total target invertebrate richness, the lack of results was surprising.

Millipedes

Millipede richness (S_{ab}) of individual Limpopo Province forests ranged from five to 11 (Table 3.7) and a total of 24 species were sampled during this study. These numbers are comparable to the millipede richness of some temperate forests in the Northern Hemisphere. According to Meyer & Singer (1997), 25 species of millipedes occur in western Austrian woodlands and individual site millipede richness ranges from four to 12 species. In the Polish Białowieża Primeval Forest, 10 to 14 millipede species occur per forest habitat, but the total millipede richness is only 14 (Wytwer & Tracz 2003). Other temperate forests support higher millipede richness than Limpopo Province forests. For example, Bonham *et al.* (2000) sampled 34 millipede species in native forests of northwest Tasmania.

A search of the South African National Millipede Database, which includes millipede localities from all national museums, some international museums and all published localities, revealed that the millipede richness of individual Limpopo Province forests are similar to the figures for South African forests in general. Richness figures for some of the best-sampled South African forests are given in Table 3.8. The high millipede richness values shown were not surprising, since the greatest number of millipede species in southern Africa occur in the eastern half, especially in forest areas (Kraus 1978).

Table 3.8: Comparative millipede richness values for relatively well-sampled forest sites in South Africa (National Millipede Database).

<i>Forest Locality</i>	<i>Province</i>	<i>Millipede richness (S)</i>
Gwaliweni Forest	KwaZulu-Natal	5
Ngeli Forest	KwaZulu-Natal	5
Swartbos (this study, least rich forest)	Limpopo	5
Mariepskop	Mpumalanga	5
Giant's Castle, Drakensberg	KwaZulu-Natal	6
Dukuduku Forest	KwaZulu-Natal	6
Cathedral Peak, Drakensberg	KwaZulu-Natal	7
Qudeni Forest	KwaZulu-Natal	7
Ngoye Forest	KwaZulu-Natal	9
Karkloof	KwaZulu-Natal	10
Nklandla Forest	KwaZulu-Natal	11
Baccarat (this study, most rich forest)	Limpopo	11
Cathkin Peak, Drakensberg	KwaZulu-Natal	12
Mazongwaan Forest	KwaZulu-Natal	13
Ngome Forest	KwaZulu-Natal	13
Champagne Castle, Drakensberg	KwaZulu-Natal	18

Centipedes

Forest centipede richness varies quite widely throughout the world, although few data have been published for most countries. The British and European centipede fauna is by far the best known (Blackburn *et al.* 2002). Within Europe, only three centipede species were recorded in a green oak forest in Toledo Province, Spain (Ruiz & Serra 2003), but 22 centipede species were collected in central Italian woodlands (Zapparoli 1992) and 28 centipede species were found in a single managed beech forest patch in Slovenia (Grgič & Kos 2003).

The centipede richness of South African sites is not well documented, especially for forests. Druce (2000) recorded three centipede species in the savanna habitat of the Greater Makalali Conservancy, Limpopo Province. According to Lawrence's (1955a) published localities, only two centipede species were recorded in Karkloof forest, KwaZulu-Natal, five centipede species occur in Franschoek Forest Reserve, Western Cape and ten centipede species were found in Tsitsikamma Forest, Eastern Cape.

In the present study, a maximum of five centipede species were recorded in a single Limpopo Province forest patch (Table 3.7) and a total of seven centipede species were sampled during this study. These figures are comparable to the above South African forest sites, although they are relatively low when compared to some of the given European figures. However, the unidentified geophilomorphs were not included in the species richness calculations, yet they comprised approximately 28% of the individuals sampled. In the Slovenia study with high centipede richness, geophilomorphs accounted for about 30% of individuals sampled (Grgič & Kos 2003).

Molluscs

The highest known terrestrial mollusc species richness in the world is found on the mid-North Island of New Zealand where 72 species are estimated to be sympatric within lowland patches of forest (Solem *et al.* 1981). However, site species richness of molluscs is usually only five to ten (Solem 1984). By these terms, the mollusc species richness of some Limpopo Province forests is exceptional, since between 11 and 15 species were recorded in seven of the sampled sites (Table 3.7). The average mollusc species richness in forests was approximately 12 and a cumulative total of 34 mollusc species were sampled during this study. In Hanglip, Entabeni and Forest Glens, 12 mollusc species were sampled in a single two by ten metre quadrat.

The majority of southern Africa's terrestrial mollusc species occur in the forest biome (van Bruggen 1978). The mollusc richness of individual Limpopo Province forests is lower than some forests in KwaZulu-Natal. Using standardised sampling, Herbert *et al.* (in prep.) sampled 22, 24, 27 and 34 mollusc species in Normandien, Ngome, Injasuti and Karkloof Forests respectively. However, mollusc sampling in KwaZulu-Natal included micromolluscs (less than five millimetres), which were not collected in the present study. The richness figures given for Limpopo Province forests only represent the minimum mollusc community in each site. Because molluscs were collected by sight and leaf litter was not examined under a microscope, most molluscs collected in this study were larger than five millimetres. However, micromolluscs can account for a large proportion of mollusc fauna in forests. For example, micromolluscs accounted for about 93% of species sampled in Madagascan rainforests (Emberton *et al.* 1996) and in Kakamega Forest, Kenya, most terrestrial mollusc species are less than five millimetres (Tattersfield, Seddon

& Lange 2001). Micromollusc sampling in Limpopo Province forests would surely increase the mollusc richness calculations considerably.

According to Solem (1984), many species of land snails can be found on islands and mountains. Like islands, mountains are isolated habitats and dissected topography, rain shadow effects, heat budget differences on shaded and exposed slopes and vegetation variations provide a multitude of niches in which speciation can occur (Solem 1984). Therefore, the high mollusc diversity calculated for Limpopo Province forests was expected.

Earthworms

Earthworm species richness across the globe varies according to geographical locality and vegetation type and ranges from one to 14 species, although two to five earthworm species is most common (Lee 1985). For example, four to ten earthworm species are sympatric within Scottish pastures (Guild 1951), but only one or two species occur together in Japanese peat bogs (Nakamura 1967).

According to Paoletti (1999), seven or eight species of earthworms are usually found in tropical and subtropical forest sites. Between four and 11 earthworm species occur together in gallery forest, Ivory Coast (Lavelle 1983). In the present study, a maximum of only two indigenous species was recorded from a single forest (Table 3.7). However, if introduced species are included, up to seven species occurred in a single forest (Grootbosch) and the average was four earthworm species per forest. The earthworm richness of Limpopo Province forests is certainly higher than that of Northwest Province pastures, where only two earthworm species occur together (Reinecke & Ljungström 1969), and Witpoortje Falls, Gauteng, where three earthworms, only one of which is indigenous, are sympatric (Pickford 1937).

The true richness of earthworms in Limpopo Province forests is probably higher than the figures presented here. Active searching of quadrats and pitfall traps only captured those species inhabiting the surface of the soil. As a result, only epigés, which live in litter, and endogés, which are active at the soil surface, were likely to be sampled. Anéciques, the large deep-burrowing earthworms, were probably underrepresented in this study. According to Lee (1985), quantitative sampling of earthworms is difficult, since

earthworms are often patchily distributed, are active at depths that vary between species and can move away from disturbances caused by sampling. Therefore, counts of field populations are most likely underestimates (Lee 1985).

Spiders

The spider richness of forest environments varies through the world. For example, 87 spider species were recorded in a German beech forest (Hoevemeyer & Stippich 2000), 89 spider species were sampled in the Belgian forest reserve 'Beiaardbos' (De Bakker *et al.* 2002) and 92 spider species were sampled in a Georgian cove forest in the United States (Dobyns 1997). Collection in the Uzungwa Scarp Forest Reserve in Tanzania yielded 170 spider species (Soerensen *et al.* 2002) and 269 spider species were recorded in montane coniferous forests in Bulgaria (Deltshev & Blagoev 1997). According to Marc *et al.* (1999), spider richness throughout the world ranges from about 40 to 150, depending upon the environment.

In the present study, a total of 70 spider species were sampled, but only between 8 and 18 species were recorded in individual forest sites (Table 3.7). Foord *et al.* (2002) recorded 127 spider species in the western Soutpansberg and a total of 59 and 73 ground-living spiders were recorded in open- and dense-understory forests respectively in Ngome State Forest, KwaZulu-Natal (van der Merwe *et al.* 1996).

When compared to these other South African forest studies, the spider species richness recorded in the present study appears low. However, the Limpopo Province forest figures are certainly only a fraction of the true spider species richness. Time and funding constraints did not allow for thorough spider sampling and plant wandering spiders were not targeted in the present study. In the western Soutpansberg, plant wanderers accounted for approximately 30% of spiders sampled by Foord *et al.* (2002) and Whitmore (2000) found that plant wandering spiders accounted for about 32% of the total spider richness in a Limpopo Province savannah ecosystem.

Comparisons of spider richness between studies can be highly misleading, since spider sampling methods are not standardised and different techniques can sample entirely different guilds. Intensively sampled sites may also appear richer than less sampled areas and some methods are not quantified. For example, in contrast to the present study, spider

sampling in the western Soutpansberg study occurred over five years, all ecological and behavioural guilds were collected and a combination of more methods (active searching, pitfall traps, sweepnetting and vegetation beating) were used (Foord *et al.* 2002). Therefore, it is not surprising that spider richness appears higher in the western Soutpansberg than in the present study, although this may only be an artefact of sampling differences.

In the significant multiple regression model presented in this chapter, forest altitude negatively affected spider species richness in Limpopo Province forests, so spider richness decreased as altitude increased. This is likely due to vegetation structure variations that correspond to altitude. Limpopo Province forests found at lower altitudes have relatively open canopies (von Maltitz *et al.* 2003) and contain more glades (pers. obs.). Such open forest environments can support higher spider species richness than closed canopies. Van der Merwe *et al.* (1996) recorded about 22% and 51% more spider species in open glades than in open- and dense-understory forests respectively in Ngome State Forest, KwaZulu-Natal. Therefore, lower altitude forests in Limpopo Province can be expected to support higher spider species richness due to their relatively open structure. This trend is clearly seen in the absolute spider richness figures (Table 3.7), where the highest spider species richness was recorded in Roodewal and Ratombo, both lower altitude semi-deciduous forests.

Amphipods

Because there was only one species indigenous to the study area, amphipods were generally considered as a presence or absence in this study. They were present in all mistbelt forests, but were not found at all in semi-deciduous forests (Roodewal and Ratombo), perhaps as a result of moisture availability or disturbance. Differing abundance of amphipods in mistbelt forests account for the variation seen in Figure 3.6c.

3.4.5 Introduced species

The presence of introduced earthworm and mollusc species in the study area was not surprising, since South African invasions by members of these two groups are documented (see Ljungström 1972a; van Bruggen 1964).

The two exotic mollusc species *Arion* sp. and *Deroceras* sp. sampled in Limpopo Province forests were considered here to be relatively unimportant. A total of only 18 individuals were sampled (one *Deroceras* sp. and 17 *Arion* sp. individuals) and they comprised less than 1% of all mollusc individuals sampled and only a small proportion of all mollusc species sampled. According to Herbert (1998), 27 species of terrestrial pulmonate molluscs have been introduced to South Africa. Although the introduced species may compete with and displace indigenous species, there is no published evidence of this having occurred in South Africa (Herbert 1997; 1998). Exotic molluscs in South African probably arrived with plants (van Bruggen 1964).

In contrast, there were significantly more introduced earthworm species in Limpopo Province forests than native species (Figure 3.9) and introduced earthworm individuals accounted for the majority of all earthworm individuals sampled. The 12 exotic earthworm species recorded in the present study are all well-known peregrine (introduced) species. Lee (1985) included *Aporrectodea* spp., *Dendrobaena* spp, *Dendrodrilus* spp., *Octolasion* spp., *Amyntas* spp., *Dichogaster boluai* (Michaelsen, 1893), *D. saliens* (Beddard, 1893) and *Pontoscolex corethrurus* (Muller, 1857), which were collected in Limpopo Province forests, in his list of the world's most widespread peregrine earthworm species.

Such high numbers of introduced earthworms in Limpopo Province forests were expected to have some negative influence on indigenous earthworm fauna. However, the forests that had the highest number of introduced earthworm species, Grootbosch and Swartbos (Figure 3.7), also had the highest number of indigenous earthworm species (2 species, Table 3.7). Grootbosch also had the second highest proportion of indigenous earthworm individuals (Figure 3.8b). This suggests that the presence of introduced earthworms have not affected indigenous fauna in forests, at least not in an overall, predictable manner. According to Lee (1985), common exotic earthworm species usually occupy niches that previously had no earthworms and there is no documented case of direct competition between established and newly introduced earthworms. Also, there is no direct evidence that peregrine earthworm species displace native species in South Africa (Ljungström 1972b). Nevertheless, we have no data pre-dating earthworm introductions in Limpopo Province forests, so we cannot know if changes in indigenous earthworm composition or abundance have occurred as a result.

The majority of earthworm introductions have occurred accidentally through the shipping of plants around the world (Lee 1985) and it is likely that exotic earthworms in South Africa arrived in the same manner (Plisko 2001). According to Plisko (2001), introduced earthworms in indigenous Limpopo Province forests are probably the consequence of *Pinus* and *Eucalyptus* plantation development in areas with good, reliable rainfall.

Multiple exotic earthworm species commonly occur together in South Africa (Plisko 2001) and not all introductions are considered to be detrimental to the environment. In particular, introductions of *P. corethrurus* (Muller, 1857), which was collected in the present study, have received much attention due to its potential beneficial role in agroecosystems (Plisko 2001). According to Hawksworth and Kalin-Arroyo (1995), introduced organisms tend to increase overall diversity on the regional level. This appears to be the case in the present study, where introduced earthworms accounted for most earthworm species sampled (Figure 3.8).

Grootbosch had the highest total number of introduced species (six species, Figure 3.7) and the lowest numbers were sampled in Goedehoop, Thathe Vondo and Forest Glens (one species, Figure 3.7). This difference may be due to varying levels of human activity within the forests. All of these forests are adjacent to plantations, but large areas of Grootbosch are divided by well-maintained roads that are used regularly by plantation workers. In contrast, there are no roads in the interior of Goedehoop, there is only one main road through the largest section of Thathe Vondo (Sacred Forest) and the single road through Forest Glens is not used regularly for plantation access.

Introductions of plant species have also been documented in Limpopo Province forests. Geldenhuys and Venter (2002) found a total of 19 exotic plant species present in Limpopo Province indigenous forests. However, none were recorded in large numbers or appeared to be invasive in the study areas.

3.5 CONCLUSION

The forest invertebrate diversity of Limpopo Province is poorly known and the present study is an important contribution to our knowledge of forest biodiversity in South Africa.

A large number of individual invertebrates comprising at least 142 indigenous species were sampled, which represent many invertebrate families and functional roles. In the South African context, the invertebrate richness of Limpopo Province forests is high, especially when considering the fact that many of the figures presented are likely to be underestimates.

Although there was no significant difference between regional (Soutpansberg forests vs. northern Drakensberg forests) species richness, diversity and evenness, there were important differences between the richness, diversity and evenness of individual forests. Each forest sampled supports a unique number and abundance of species and forests rank differently depending upon the target invertebrate group considered. With the exception of spiders, the factors influencing total and individual target group richness could not be determined, which indicates that the processes driving invertebrate richness are likely to be complex and are beyond the scope of the present study. Introduced invertebrates, most of which were earthworms, comprised a large proportion of the species and individuals sampled, but have not been shown to affect indigenous fauna.

Although this chapter has presented information that can be used to prioritise forests for conservation, none of the measures consider the identity of species and similar numbers do not indicate similar communities. As a result, this information is of limited value in community comparison and for practical applications in conservation.

CHAPTER 4

INVERTEBRATE COMMUNITIES, DISTRIBUTION AND BIOGEOGRAPHY

4.1 INTRODUCTION

Biogeography can be defined simply as the branch of science concerned with plants and animals and their patterns of distribution (Meadows 1985). By examining the distributions of organisms, scientists can (1) identify affinities between different areas; (2) determine the processes that influence distribution; (3) model historical changes in distributions; (4) locate areas where diversity, endemism or relict faunas are concentrated and (5) develop theories to explain colonisation and extinction of species (Meadows 1985; Burgess *et al.* 1998).

All of these aspects of biogeography have important applications in conservation. According to Hawksworth and Kalin-Arroyo (1995), knowledge of distribution patterns leads to prediction and prediction provides the basis for taking action. For example, knowledge of the processes that determine species composition might help us predict the consequences of habitat fragmentation or resource utilisation (Bond 1989b). Biogeographic theory could be used to estimate the number of species that may be lost if the area of a nature reserve was reduced (Meadows 1985). Historical changes in distributions could be used to predict the effects of future climate change (Eeley *et al.* 1999). Species' distributions could be used to identify important centres of diversity and endemism that need protection (Hawksworth & Kalin-Arroyo 1995).

In this chapter I examine the distribution patterns of target forest invertebrates and the processes that determine the species' distributions. Similarity analyses are presented for forests, vegetation subtypes and regions, patterns of endemism are evaluated and historical influences on the invertebrate distributions in Limpopo Province forests are investigated. Some current biogeographic theories are also tested in terms of Limpopo Province forest invertebrate species. Each of these analyses is presented to identify forests of conservation priority and to determine the factors and processes that contribute to the conservation value (i.e. endemic and unique species) of Limpopo Province forests.

4.1.1 Measuring beta diversity

Beta (β) or between-habitat diversity is a measure of how the species compositions of samples, habitats or communities differ. Beta diversity increases as different communities share fewer species (Magurran 1988). Beta diversity can be quantified using presence and absence data with methods such as Whittaker's measure (Whittaker 1960), Routledge's measures (Routledge 1977) and Wilson and Shmida's measure (Wilson & Shmida 1984). However, these methods describe beta diversity only in terms of transects or environmental gradients (Magurran 1988). Alternatively, the degree of association or similarity of sites or samples can be measured using standard ecological techniques of ordination and classification (Southwood 1978).

The beta diversity of site pairs is most easily measured by using similarity coefficients, such as the Jaccard index and the Sorensen index (Southwood 1978; Magurran 1988). The Jaccard index, which I use in this chapter, is calculated with the following formula:

$$C_j = j / (a + b - j)$$

Where

- a = total number of species in Site A
- b = total number of species in Site B
- j = number of species found in both Site A and B

This index equals '1' when sites are completely similar and '0' when sites are dissimilar and have no common species. Similarity coefficients such as the Jaccard index are simple, but take no account of species abundance and all species are counted equally regardless of rarity (Magurran 1988).

Another method of beta diversity investigation is cluster analysis, which can be used when there are a number of sites to be compared. This method combines similar sites into groups or 'clusters' that are arranged in a hierarchical structure called a dendrogram (Ludwig & Reynolds 1988). Cluster analysis is designed to reveal natural groupings of sites that would otherwise not be apparent (Norusis 1994). Starting with a matrix giving the similarity between each pair of sites, this analysis first groups the two most similar sites then progressively clusters sites until they are combined into a single dendrogram. The

height of each node (where a new cluster is formed) indicates the degree of similarity for that cluster. Cluster analysis can be performed with either presence or absence data or quantitative data, although in many cases the results are nearly identical (Magurran 1988). I also use cluster analysis in this chapter to express beta diversity.

4.1.2 Species endemism

Animal species' distributions are influenced by many factors, including historical and ecological processes and some species-specific biological and behavioural characteristics. These characteristics include reproductive strategies, reproductive behaviour, territorial behaviour, vagility, food requirements and the distribution of critical natural resources (Miller 1994). Because species have differential requirements, characteristics and biogeographic and evolutionary histories, distributions can vary considerably from species to species. Some species are found over large geographic areas while others have more restricted distributions.

Endemic species are those found in only one area and nowhere else (Spellerberg 1996a) and endemism is the product of historical factors, environmental heterogeneity, taxon mobility and isolation (Hawksworth & Kalin-Arroyo 1995). Past studies on endemism have focused largely on vascular plants, birds and butterflies, on island endemics and on known centres of endemism (Hawksworth & Kalin-Arroyo 1995; Spellerberg 1996a). Because the areas of restriction can vary dramatically, endemism is a relative concept and endemic status can have varying significance depending upon the size and location of the area under consideration (Hawksworth & Kalin-Arroyo 1995).

Endemics are commonly categorized according to their spatial distribution and can be assessed on many different scales. According to Hawksworth & Kalin-Arroyo (1995), it is important to be unambiguous about defining and categorizing endemism and data should be presented at several scales to enable comparisons to be made among taxa. When choosing appropriate scales for assessing endemics, the mobility of the taxa under consideration must always be taken into account (Hawksworth & Kalin-Arroyo 1995). To obtain meaningful results, mobile taxa should be categorized on larger scales than less mobile taxa. For example, the International Council for Bird Preservation (1992) identifies endemic birds by a 50 000 square kilometre criterion. In contrast, endemism in less mobile

invertebrates can be categorized at much smaller scales, such as a 10 kilometre criterion for site endemics (Hamer & Slotow 2002).

According to Hawksworth & Kalin-Arroyo (1995), endemism is influenced by taxonomic interpretation, sampling error and human perceptions of rarity. Therefore, limited geographic exploration and taxonomic inconsistencies can bias the identification of endemics and the significance of their status (Kruckeberg & Rabinowitz 1985). Endemics identified as a result of inadequate or uneven sampling and excessive taxonomic splitting are called ‘pseudoendemics’ (Nelson *et al.* 1990; Crowe *et al.* 1994).

Endemism can be expressed as a percentage of all taxa present or as the absolute number of endemics in an area (Hawksworth & Kalin-Arroyo 1995). In this chapter, I investigate invertebrate species endemism in Limpopo Province forests at four levels and characterize the amounts of endemism in the two regions, the three vegetation subtypes and the eleven individual forests. I also evaluate some factors that influence species endemism in Limpopo Province forests.

4.1.3 Limpopo Province forest history in brief

According to Hawksworth and Kalin-Arroyo (1995), studies of distributional patterns of diversity have shown that every region has had a unique phylogenetic, geographic and ecological history that has shaped its present day diversity. Strong correlations in diversity patterns may reflect history rather than outcomes of species interactions. Therefore, emphasis must be placed on understanding the local processes and history of a community and on the assessment of the relationship of that community to others nearby.

The Limpopo Province forests have an interesting biogeographical history. These forests lie just south of the Limpopo River valley, which has probably acted as a significant barrier to the southward radiation of species from tropical African regions (Poynton 1961; Poynton 1989; Lawes 1990; Clancey 1994). As a result, the forest species of the Limpopo Province have apparently been sourced from Afrotropical assemblages within South Africa and represent a northward radiation of species (Lawes 1990; Clancey 1994).

The distribution patterns of contemporary forest species in southern Africa are largely assumed to be a result of vegetation adjustments following climatic changes during the Quaternary (van Wyk 1989; Lawes 1990). Throughout the Pleistocene epoch, the expansion and shrinking of the polar ice caps were reflected by severe changes in the global climate that exerted major environmental pressures on Africa's flora and fauna (Huntley 1988).

The last hypothermal (last glacial maximum) occurred approximately 18 000 years ago and created cooler and generally drier climates than present (Deacon 1983, Deacon *et al.* 1983). The climatic changes during this time probably reduced forests in South Africa to a very patchy Afrotemperate forest archipelago to the south of Limpopo Province (Lawes 1990, Eeley *et al.* 1999). Forest remnants were likely restricted to the Eastern Cape, but could have also occurred in Mpumalanga and in lower altitudes of KwaZulu-Natal (coastal scarp forests), and they formed important refugia for some forest populations (Lawes 1990).

Temperatures increased quite rapidly following the last glacial maximum after about 16 000 years ago with temperatures peaking during the Holocene altithermal (circa 4500-7000 BP, Partridge *et al.* 1990). Afromontane forests in South Africa were likely to have expanded in response to the more favourable climates (Meadows & Linder 1989; Lawes 1990, Eeley *et al.* 1999). However, the Limpopo region was drier during this time than at present (Partridge 1997) and forests in the area only expanded following the altithermal when slightly cooler and wetter conditions predominated in the region (Scott, L. 1987).

The expansion of forests during the Holocene would have reduced the effectiveness of dispersal barriers to the south of Limpopo Province and forest fauna would have radiated out of southern forest refugia (Lawes 1990). However, the arid Limpopo River valley remained a significant barrier throughout the Holocene (van Zinderen Bakker 1978) and could have prevented the movement of forest species into South Africa from the north. According to van Bruggen (1967), the Limpopo River was and is a significant barrier, particularly for montane forest invertebrates. As a result, the contemporary Limpopo Province forest species compositions are likely to be southern and temperate in origin (Midgley *et al.* 1997).

In this chapter I determine if this biogeographic pattern is evident in invertebrate communities by comparing the invertebrate assemblages of Limpopo Province, KwaZulu-Natal and eastern Zimbabwean forests.

4.2 METHODS

Invertebrates from the seven target taxa were sampled according to the three sampling methods in 11 forest patches in Limpopo Province as described in Chapter 2. Only indigenous species are included in these analyses.

4.2.1 Site similarity

Limpopo Province forest invertebrate communities were compared using the Jaccard index (see formula in Section 4.1.1) and all calculations were performed using a calculator. All target indigenous invertebrates sampled in quadrats, pitfalls and transects were included.

To compare forests patches, Jaccard indices were calculated for all possible forest pair combinations and were based on species shared between forests and on families shared between forests. A second analysis was performed to compare the total Soutpansberg species and family composition to each individual Drakenberg forest and vice-versa. Jaccard indices were calculated for species shared and families shared between each Drakensberg forest and the whole Soutpansberg region. Likewise, Jaccard indices were calculated for species shared and families shared between each Soutpansberg forest and the whole Drakensberg region.

4.2.2 Cluster analysis

Cluster analysis was also used to compare the species composition of forests. All indigenous target invertebrates sampled in quadrats, pitfalls and transects were included in this analysis. Dendrograms were generated with the statistical program SPSS (Norusis 1994), using the between-groups method and measure of Euclidean distance. This analysis was first performed for all target group species sampled and then for the species sampled in each individual target group.

4.2.3 Species endemism analysis

Patterns of species endemism were determined by examining the distributions of sampled species in each target group. The distributions of species from target taxa were obtained from the following sources:

- Millipedes: Hamer 1998; 2000
- Centipedes: Lawrence 1955a; 1984
- Earthworms: Pickford 1937; Plisko 1997; Natal Museum Earthworm Database and J. D. Plisko 2003, pers. comm.
- Molluscs: van Bruggen 1965; 1967; van Mol & van Bruggen 1971; Natal Museum Mollusc Database and D. Herbert 2002, pers. comm.
- Spiders: A. S. Dippenar-Schoeman 2002, pers. comm.
- Amphipods: Griffiths 1999

Species identified in this study as ‘cf’ are possibly new species, but were considered here to be synonymous with the described species and are included in this analysis. Although they are not yet described, new species discovered during this study were also included and their distributions were determined by sampling for this project. Species that could not be identified, such as *Chaleponcus* ‘species 1’ are excluded from this analysis, since distribution data cannot be obtained for these species.

Endemism was defined at a number of scales using logical breakpoints. The four classes of endemism chosen for this study are as follows: (1) *Site endemics*, including all species with only one forest locality. (2) *Local endemics*, including all species restricted to the forests of only one mountain chain, i.e. the Soutpansberg or northern Drakensberg. (3) *Regional endemics*, including all species restricted to Limpopo Province forests. (4) *National endemics*, including all species restricted to South Africa in both forests and non-forested habitats.

One way ANOVAs and LSD post hoc tests were used to identify significant differences between the number of endemic species in forests, regions (Soutpansberg and northern Drakensberg) and forest subtypes. Sample sizes were not equal between regions and forest subtypes, so comparisons were based on mean values that were independent of sample size. All statistical analyses were performed in SPSS (Norusis 1994) and Kolmogorov-

Smirnov goodness of fit tests were used to determine the normality of the data distribution. Each analysis was performed at two scales: (1) *All endemics*, including species fulfilling the criteria for all four prescribed levels and (2) *Limpopo Province forest endemics*, including only regional, local and site endemics. Finer scale analysis on local or site levels could not be performed because the numbers of local and site endemics were too small for meaningful comparisons.

Linear regression was used to determine if a relationship exists between the number endemics in Limpopo Province forests and the distance from likely sites of Pleistocene forest refugia (or connectivity to the regional species pool). Only local and site endemics were considered, since the national endemic level includes some relatively widely distributed species and species that occur in forested and non-forested areas. The regional endemic level was not included because its species are too broadly distributed for meaningful comparisons on the scale of forest. Because our knowledge of climate and vegetation change during the Pleistocene is limited (van Zinderen Bakker 1978), the precise forest refuge sites are unknown. Therefore, the distance of the Soutpansberg and northern Drakensberg from a possible site of forest refuge was measured in two ways. Two locations were used as sites of forest refuge: (1) Ngome Forest, KwaZulu-Natal. This is a mist belt forest and is located in an important forest refuge area (Eeley *et al.* 1999). (2) Mariepskop Forest, Mpumalanga. This forest is found within the Drakensberg range and is the nearest relatively large forest patch to the study site. Distances between each forest pair were obtained from a map of southern Africa. First, linear regression was used to determine the relationship between target group species richness and the number of local and site endemics in forests. Any forests that were outliers from this regression line were removed from the subsequent analysis. Second, species richness, individual forest isolation and forest size were all factored out of the regression using residuals before determining the relationship.

4.2.4 Comparison with Zimbabwean and KwaZulu-Natal forests

Further biogeographic trends were examined by comparing the invertebrate fauna of Limpopo Province forests with similar forests to the south (KwaZulu-Natal Afromontane forests) and to the north (forests in the eastern highlands region of Zimbabwe). Only millipedes and molluscs were considered for this analysis because they were sufficiently diverse at several taxonomic levels (family, genus and species) and Zimbabwean forest distribution records for these groups were relatively numerous.

Millipedes

Millipede species' localities were obtained from Hamer (1998). All millipedes recorded in the KwaZulu-Natal Drakensberg forests (Giant's Castle, Cathedral Peak, Champagne Castle, Cathkin Peak, Royal Natal National Park), Karkloof and Ngeli Forest were included as KwaZulu-Natal forest species. These Afromontane forests were selected because they are relatively well-sampled. The Zimbabwean forest millipede species list included all species recorded from the eastern highlands regions of Zimbabwe, including the Chimanimani Mountains, Chirinda Forest, Salone Forest, Chipinge, Inyanga and Mutare. The Soutpansberg and Drakensberg millipede species lists included all species sampled in this study along with nine additional species previously recorded from the study area (Hamer 1998).

Three millipede orders, Polyxenida, Polyzoniida and Siphonophorida, were excluded from this analysis because they are small-sized, relatively obscure and have low diversity (Hamer & Slotow 2002). These orders were only represented in the KwaZulu-Natal forest millipede species list, probably because KwaZulu-Natal is the most intensively surveyed province in South Africa (Hamer & Slotow 2002). Limpopo Province and Zimbabwean forests have been sampled to a lesser degree.

Comparisons were made at the level of genera based solely on logic. Species were not used to compare these regions because millipedes have high levels of species endemism (Hamer & Slotow 2002) and 55% of millipedes sampled in this study are restricted to Limpopo Province forests. Therefore, lines of affinity had to be sought at a higher taxonomic level. Families were not used since they can be alike across large regions and even continents (M. L. Hamer 2003, pers. comm.).

Listed millipede genera were entered into a matrix that indicated presence or absence in each region. These data were then subjected to cluster analysis and a dendrogram was generated in SPSS (Norusis 1994), using the between-groups method and measure of Euclidean distance. Jaccard similarity coefficients were also calculated for each pair of regions.

Molluscs

Mollusc species localities were determined from the Natal Museum Mollusc Database, published literature (van Bruggen 1971; 1980) and from A. C. van Bruggen (2003, pers. comm.). All molluscs recorded from Karkloof forests were included as KwaZulu-Natal forest species. Karkloof was selected because it has the highest number of records and is the best-sampled forest in KwaZulu-Natal. Additional KwaZulu-Natal forests were not considered because the list of species would be disproportionately long and would confound comparisons. The Zimbabwean forest mollusc species list included all molluscs recorded from the Vumba Mountains, Chirinda Forest and Inyanga. Eighteen mollusc species previously recorded from the study area (Natal Museum Mollusc Database) were added to the species sampled in the present study to comprise the Soutpansberg and Drakensberg mollusc species lists.

Because mollusc species were more widespread than millipede species, comparisons were made on both the species and genus levels. Mollusc species and genera lists were entered into a presence or absence matrix for each region. Cluster analysis was then used to compare the species and genera composition of regions. As for millipedes, dendrograms were generated with SPSS (Norusis 1994), using the between-groups method and measure of Euclidean distance, and Jaccard similarity coefficients were calculated for each pair of regions, but comparisons of mollusc composition were made on both the species and genus levels.

4.3 RESULTS

4.3.1 Site similarity

Jaccard similarity coefficients were calculated for target invertebrate species shared by each forest pair. The species composition of forests varied considerably; coefficients ranged in value from 0.10 to 0.50 and patterns in similarity were not immediately apparent. All values obtained are given in Appendix 8. To simplify interpretation, only pairs of sites sharing 30% or more of their species were included in Table 4.1a. These figures represent the upper half of all values.

The greatest species similarity was found between forests pairs sharing the mistbelt forest subtype and pairs within the northern Drakensberg region. Although not all mistbelt forest pairs shared 30% or more of their invertebrate species, all pairs showing such similarity were of the mistbelt forest subtype. The two semi-deciduous forests, Roodewal and Ratombo, shared less than 30% of their species with each other and all of the mistbelt forests. All Drakensberg forest pairs were quite similar in species composition, as were all mistbelt forest pairs in the Soutpansberg except the Goedehoop:Hanglip pair. Grootbosch, the largest forest sampled in this study, shared 30% or more of its species with all other mistbelt forest sampled, including those in the Drakensberg and in the Soutpansberg.

Even though there were some similarities in the species composition of forest pairs, all three forest subtypes had unique species. To clarify these results, the mistbelt forest subtype was divided according to region into Soutpansberg mistbelt forests and Drakensberg mistbelt forests. The Drakensberg mistbelt forests had the greatest number of unique species, while the semi-deciduous mixed forests had the lowest number (Figure 4.1a).

Jaccard similarity coefficients were also calculated for target invertebrate families shared by forest pairs. Coefficients ranged in value from 0.34 to 0.74 and all values are presented in Appendix 9. To simplify interpretation, only forest pairs sharing more than 55% of invertebrate families are shown in Table 4.1b. These given values represent the highest half all values obtained.

Overall, family similarity between forest pairs was greater than species similarity, as reflected in the larger coefficients obtained. Results for the family level were similar to the species figures, but several differences are evident. All Drakensberg forest pairs shared 55% or more of their families, except for the New Agatha:Forest Glens and Swartbos:Forest Glens pairs. Only half of the Soutpansberg mistbelt forest pairs shared 55% or more of their families. Grootbosch shared 55% or more of its families with all other forests except Ratombo. The invertebrate family composition of Baccarat was also similar to many other forests, sharing 55% or more of its families with all other mistbelt forests. Although the semi-deciduous forests Roodewal and Ratombo were not similar on the species level to each other or any mistbelt forest, high degrees of family similarity were present between the Roodewal:Forest Glens, Ratombo:Grootbosch and Ratombo:Swartbos pairs.

Despite the similarities in the family composition of some forest pairs, two of the three forest subtypes had families that were not found in any other forest subtype. After dividing the mistbelt forest subtype by region, it was shown that the Drakensberg mistbelt forests had the most unique families, followed by the Soutpansberg mistbelt forests and the semi-deciduous scrub forest (Roodewal). Only the semi-deciduous mixed forest (Ratombo) did not have any unique families (Figure 4.1b). Each individual mistbelt forest also had unique species and six of the nine mistbelt forests even had families unique to that forest patch (Figure 4.2).

Jaccard similarity coefficients were calculated for species and families shared between forest regions and individual forests. The target invertebrate composition of the whole Soutpansberg region was compared to each individual Drakensberg forest and the target invertebrate composition of the whole Drakensberg region was compared to each individual Soutpansberg forest. The values obtained are presented in Figure 4.3.

On the species level, Grootbosch was most similar to the Soutpansberg forests, while Forest Glens was the least similar. These forests are the closest and furthest from the Soutpansberg respectively. However, family composition did not mirror these trends and Baccarat was most similar to the Soutpansberg on the family level while Swartbos, Baccarat's nearest neighbour, was the least similar (Figure 4.3a). Hanglip's species and family composition were most similar to the Drakensberg forests, even though it is

relatively distant from the region. On the species level, Roodewal was the least similar to the Drakensberg and Ratombo was the least similar on the family level (Figure 4.3b).

Table 4.1: Similarities in invertebrate family and species composition between Limpopo Province forests. Jaccard similarity coefficients are given for forests sharing a) 30% or more of their invertebrate species and b) 55% or more of their invertebrate families. All values have been multiplied by 100 for ease of interpretation. Forest names are abbreviated as follows: Hanglip = HAN, Roodewal = ROD, Goedehoop = GHP, Ratombo = RAT, Entabeni = ENT, Thathe Vondo = TV, Grootbosch = GRO, New Agatha = NAG, Swartbos = SWB, Baccarat = BAC, Forest Glens = FGL.

Site	HAN	ROD	GHP	RAT	ENT	TV	GRO	NAG	SWB	BAC	FGL
a) HAN	-										
ROD		-									
GHP			-								
RAT				-							
ENT	43		37		-						
TV	50		31		44	-					
GRO	30		30		39	33	-				
NAG							37	-			
SWB						30	43	37	-		
BAC	30						42	37	40	-	
FGL	38					30	42	39	33	39	-
b) HAN	-										
ROD		-									
GHP			-								
RAT				-							
ENT	58				-						
TV	61				59	-					
GRO	59		59	63	57	65	-				
NAG							57	-			
SWB				61			68	67	-		
BAC	58		64		56	59	74	61	61	-	
FGL	64	63			57		57			57	-

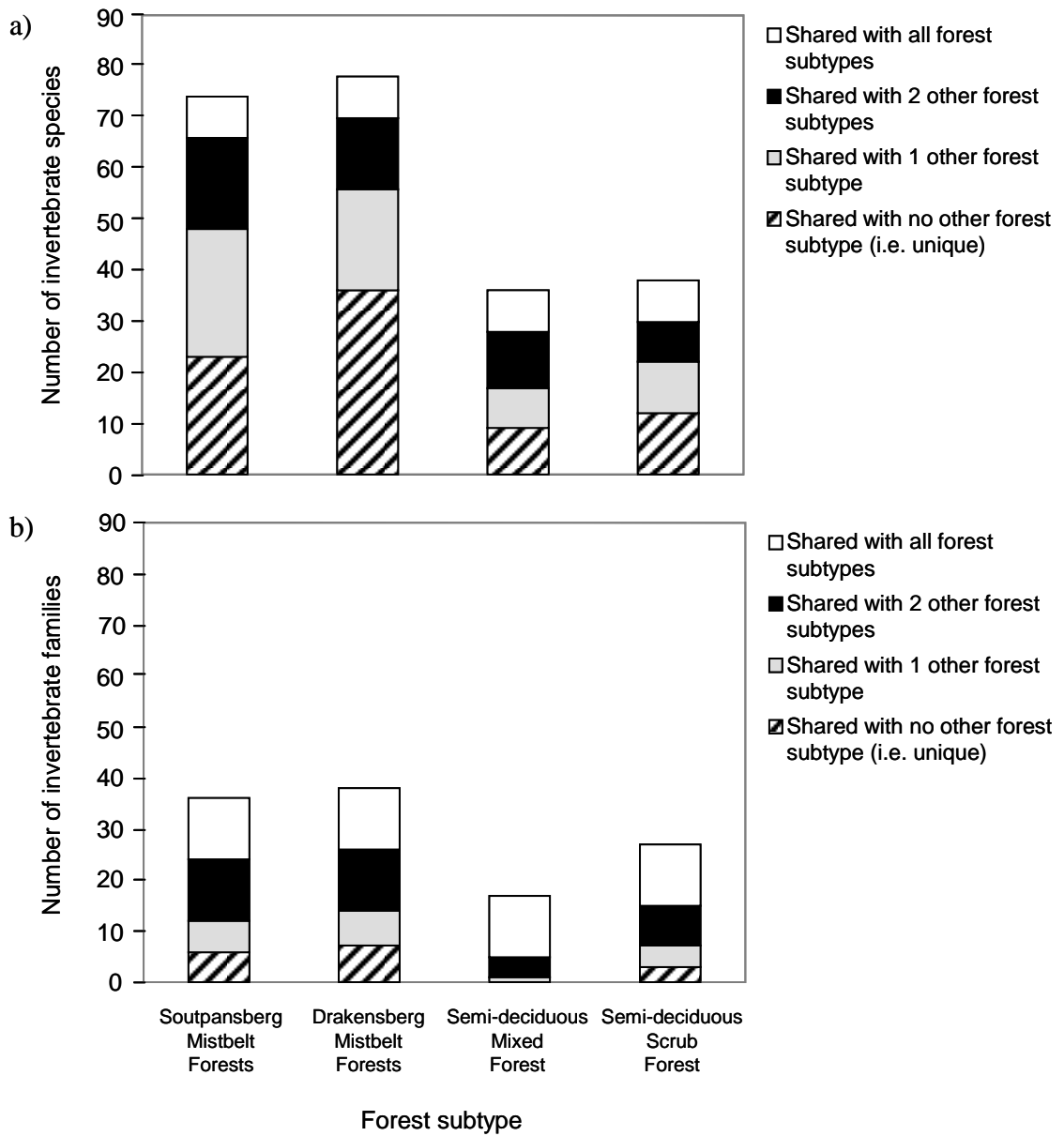


Figure 4.1: The contribution of the three Limpopo Province forest subtypes to invertebrate richness where a) is the species composition and b) is the family composition. The mistbelt forest subtype has been divided according to region.

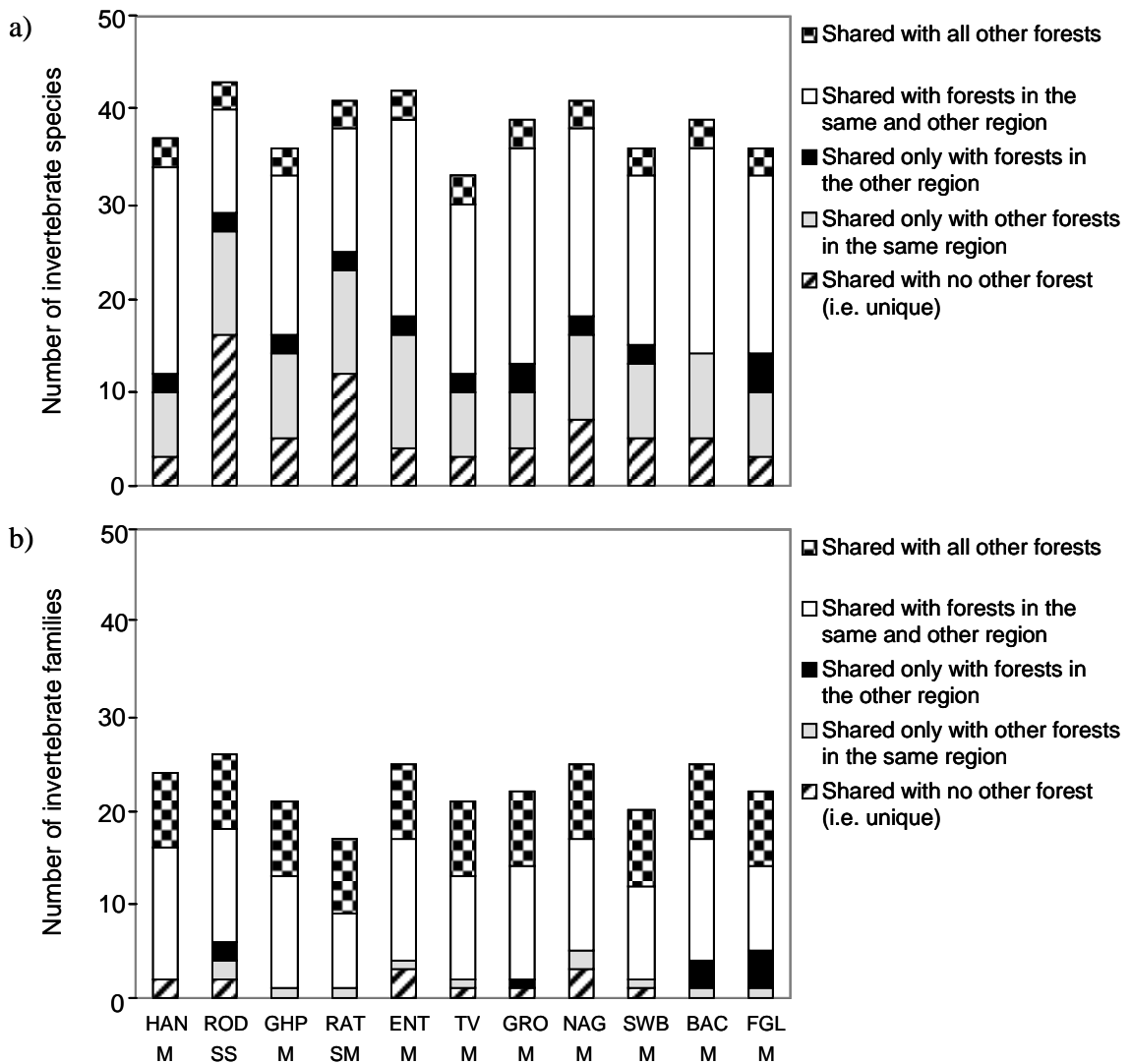


Figure 4.2: The contribution of each forest sampled in Limpopo Province to invertebrate diversity where a) is the species composition and b) is the family composition. Forest names are abbreviated as follows: Hanglip = HAN, Roodewal = ROD, Goedehoop = GHP, Ratombo = RAT, Entabeni = ENT, Thathe Vondo = TV, Grootbosch = GRO, New Agatha = NAG, Swartbos = SWB, Baccarat = BAC, Forest Glens = FGL. Forest names are coded by vegetation subtype (M = mistbelt forest, SS = semi-deciduous scrub forest, SM = semi-deciduous mixed forest).

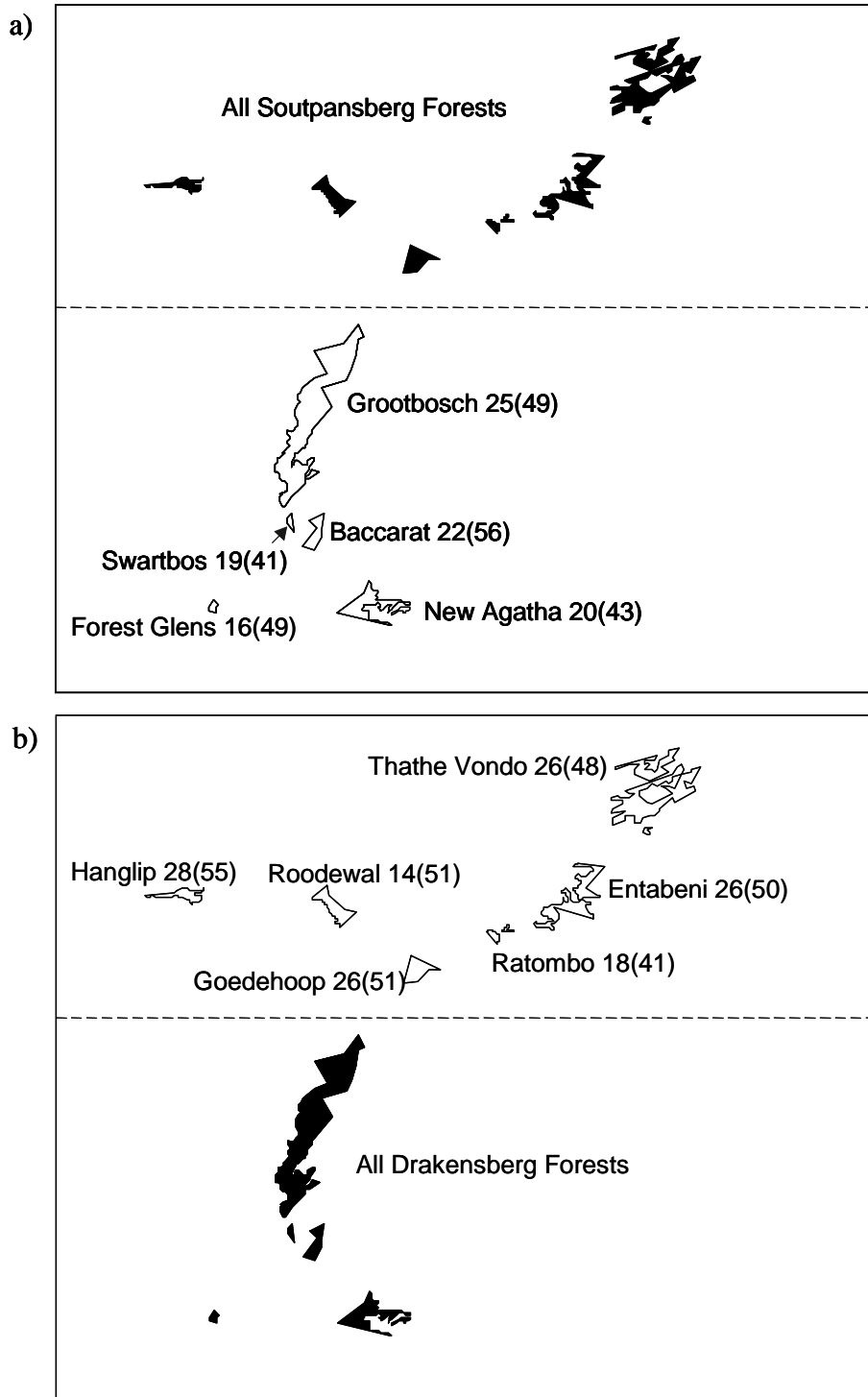


Figure 4.3: Comparison of the invertebrate composition of forest regions with individual forests. Jaccard similarity coefficients for the number of species and (families) shared between a) all Soutpansberg forests and each forest sampled in the Drakensberg and b) all Drakensberg forests and each forest sampled in the Soutpansberg. All values have been multiplied by 100 for ease of interpretation. Dotted lines indicate where map areas have been removed. See Figure 2.1 (pg. 36) for actual distances between regions.

4.3.2 Cluster analysis

When all target invertebrate species were included, forests were clustered by vegetation subtype and region and two main clusters were formed. Cluster A contained all mistbelt forests in the Soutpansberg and cluster B included all Drakensberg mistbelt forests. These two clusters were combined to form a single group containing all mistbelt forests sampled. The two semi-deciduous forests, Roodewal and Ratombo, were outliers (Figure 4.4a).

The dendrograms generated for each individual target group in forests (Figures 4.4b, 4.4c and 4.5) showed groupings similar to those of all target invertebrates (i.e. groupings by forest subtype and region), but the numbers of main clusters varied from two (spiders) to four (earthworms and millipedes). The dendrograms for centipedes and molluscs each included a main cluster that contained both Soutpansberg and Drakensberg forests and the earthworm dendrogram included three cross-regional clusters. The greatest degree of dissimilarity between forests occurred in the dendrogram for spiders.

4.3.3 Species endemism analysis

A total of 47 endemic invertebrate species were identified from distribution data (Appendix 10). These accounted for approximately 53% of all identified indigenous target group species. Each endemic species was classified according to the four prescribed levels. There were six site endemics, eight local endemics, nine regional endemics and 24 national endemics recognized from the six target taxa. Figure 4.6 shows the levels of endemism found in each taxon, excluding introduced species and those species that could not be identified. Limpopo Province forest endemics accounted for 26% of all identified indigenous target group species and approximately 22% when introduced species are included.

SPSS (Norusis 1994) was used in all stages of this analysis and in all cases the assumptions of the ANOVA were met (Komogorov-Smirnov test $P > 0.05$).

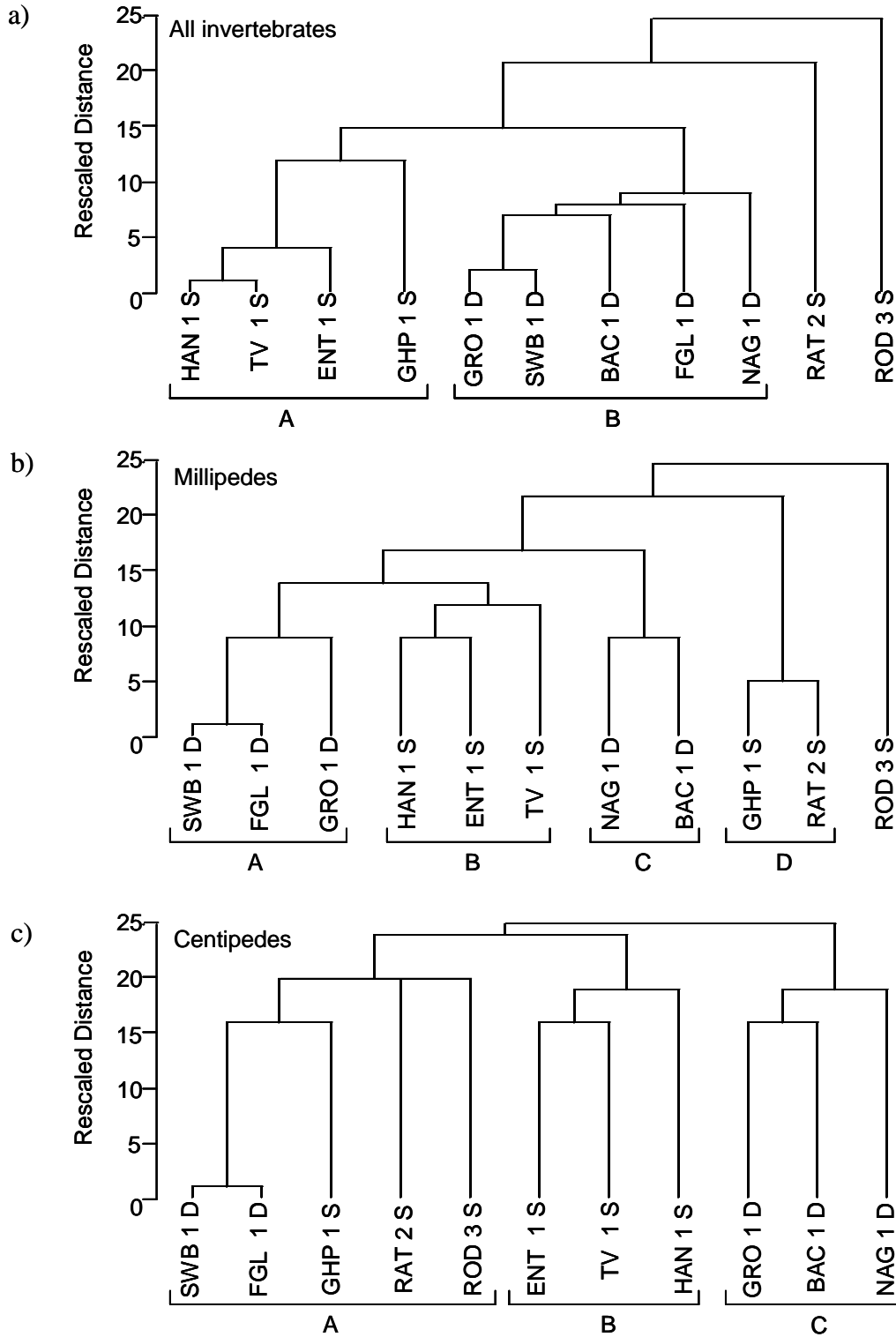


Figure 4.4: Dendrograms for a) all target invertebrate species, b) millipede species and c) centipede species shared between forests using the average linkage between forests and Euclidean distances. Forest names are abbreviated as follows: Hanglip = HAN, Roodewal = ROD, Goedehoop = GHP, Ratombo = RAT, Entabeni = ENT, Thathe Vondo = TV, Grootbosch = GRO, New Agatha = NAG, Swartbos = SWB, Baccarat = BAC, Forest Glens = FGL. Forests are coded by vegetation subtype (1 = mistbelt forest, 2 = semi-deciduous mixed forest, 3 = semi-deciduous scrub forest) and region (S = Soutpansberg, D = Drakensberg).

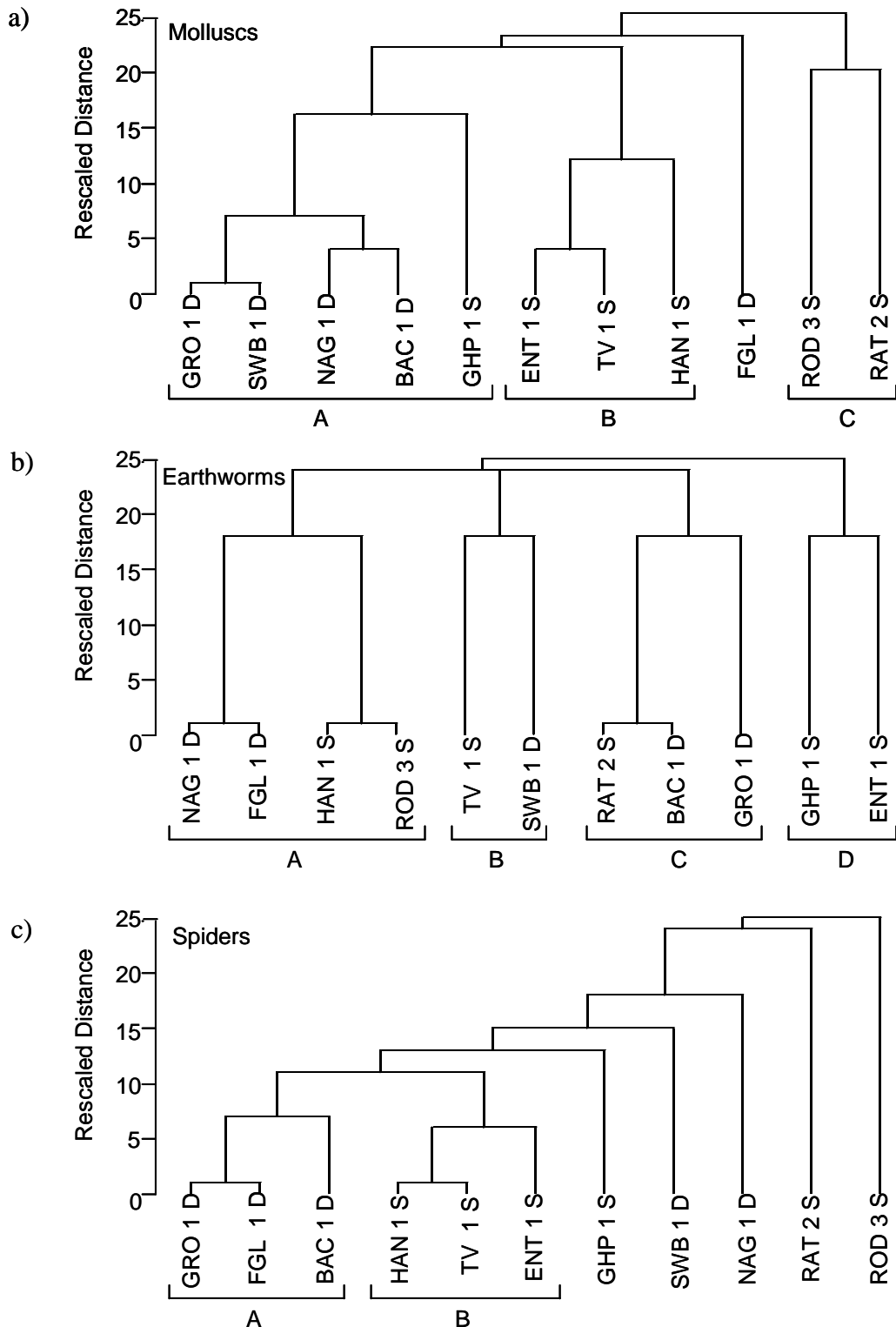


Figure 4.5: Dendrograms for a) mollusc, b) earthworm and c) spider species shared between forests using the average linkage between forests and Euclidean distances. Forest names are abbreviated as follows: Hanglip = HAN, Roodewal = ROD, Goedehoop = GHP, Ratombo = RAT, Entabeni = ENT, Thathe Vondo = TV, Grootbosch = GRO, New Agatha = NAG, Swartbos = SWB, Baccarat = BAC, Forest Glens = FGL. Forests are coded by vegetation subtype (1 = mistbelt forest, 2 = semi-deciduous mixed forest, 3 = semi-deciduous scrub forest) and region (S = Soutpansberg, D = Drakensberg).

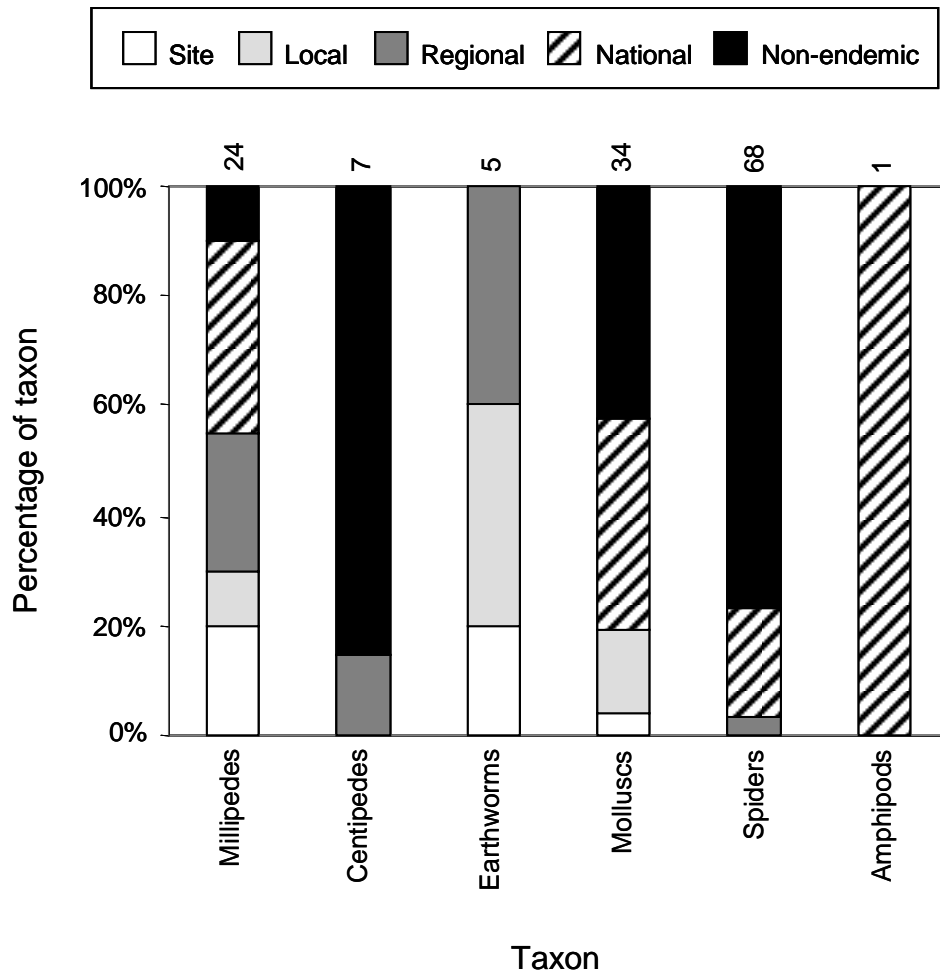


Figure 4.6: Levels of endemism in six target taxa in all Limpopo Province forests sampled, excluding introduced species and those species that could not be identified. Figures above each bar indicate the total number of indigenous species identified in each taxon.

Endemism by region

Regional endemism was examined at two scales: (1) all endemics and (2) Limpopo Province forest endemics. The northern Drakensberg had significantly more endemic species than the Soutpansberg at both scales (1: $F_{1,54} = 14.281$, $P < 0.001$, 2: $F_{1,54} = 20.287$, $P < 0.001$, Figure 4.7). When only mistbelt forests were considered, the Drakensberg still had significantly more endemic species than the Soutpansberg at both scales (1: $F_{1,44} = 4.311$, $P = 0.044$, 2: $F_{1,44} = 8.624$, $P = 0.005$).

Endemism by forest subtype

Forest subtype endemism was also examined at the above two scales. When all endemic species were considered, there was a significant difference between the numbers of endemics in forest subtypes ($F_{1,54} = 13.458$, $P < 0.001$, Figure 4.8). At this scale, mistbelt forests had significantly more endemic species than semi-deciduous mixed forests (post hoc test LSD, $P = 0.001$) and semi-deciduous scrub forests (post hoc test LSD, $P < 0.001$). There was no significant difference between the numbers of endemics in the two semi-deciduous forest subtypes (post hoc test LSD, $P = 0.676$).

Results were similar when only Limpopo Province forest endemics were considered. There was also a significant difference between the numbers of endemic species in the three forest subtypes ($F_{1,54} = 30.145$, $P < 0.001$, Figure 4.8) and mistbelt forests had significantly more endemics than semi-deciduous mixed forests (post hoc test LSD, $P = 0.001$) and semi-deciduous scrub forests (post hoc test LSD, $P < 0.001$). However, at this scale semi-deciduous mixed forests had significantly more endemic species than semi-deciduous scrub forests (post hoc test LSD, $P = 0.007$).

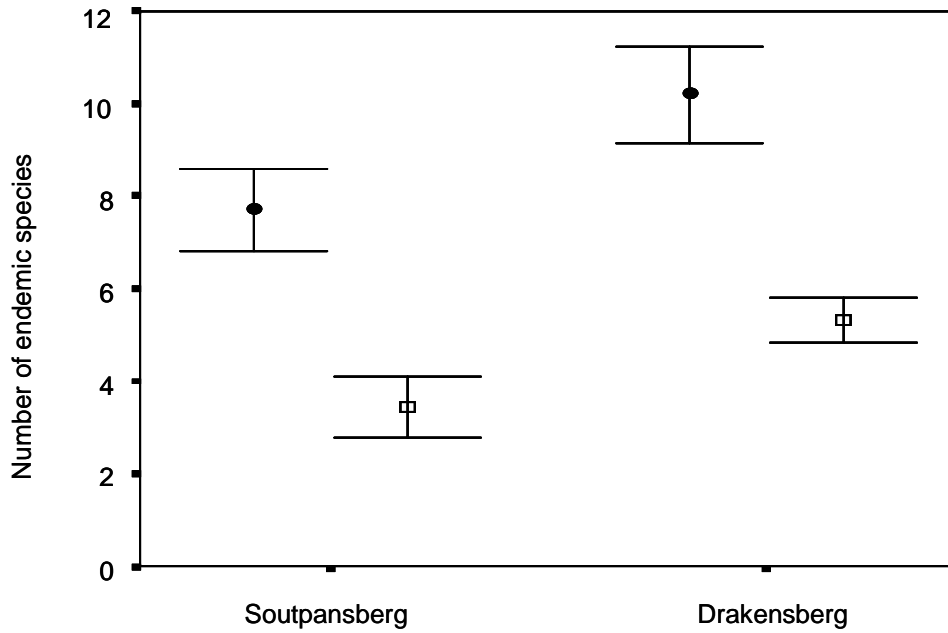


Figure 4.7: The number of endemics and 95% confidence limits for each region sampled, with the total number of endemics (all levels, ●) and Limpopo Province forest endemics (regional, local and site levels, □).

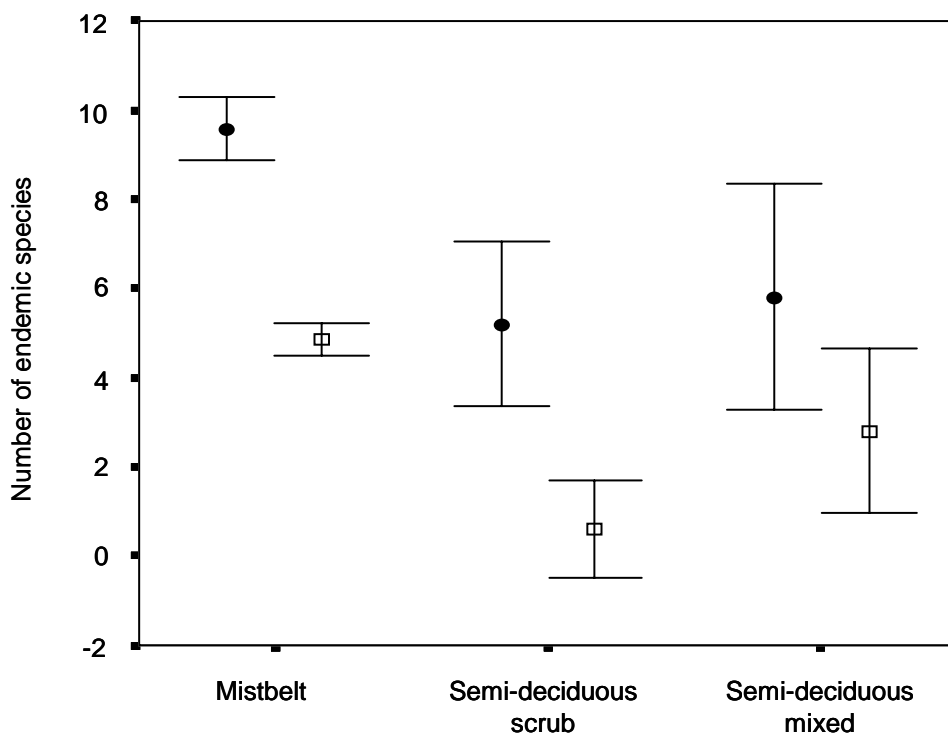


Figure 4.8: The number of endemics and 95% confidence limits for each forest subtype sampled, with the total number of endemics (all levels, ●) and Limpopo Province forest endemics (regional, local and site levels, □).

Endemism by forest

The number of endemic species sampled in each forest varied, as did the taxonomic assemblage of endemics. Figure 4.9 shows the contribution of each taxon to the total number of endemic species recorded in each forest and Figure 4.10 shows the numbers and levels of endemic species sampled in each forest.

Forest endemics were compared on the two scales. When all endemics were included, there was a significant difference between the numbers of endemic species in forests ($F_{1,54} = 4.958$, $P < 0.001$, Figure 4.11). There was also a significant difference between Limpopo Province forest endemic numbers ($F_{1,54} = 8.207$, $P < 0.001$, Figure 4.11). However, post hoc test revealed that differences between individual forests varied according to scale (Table 4.2).

Entabeni, Forest Glens and New Agatha had the highest numbers of endemic species and Roodewal and Ratombo had the lowest numbers when all endemics were considered (absolute figures). The highest numbers of Limpopo Province forest endemics were found in Entabeni, Baccarat and New Agatha and the lowest number was recorded in Roodewal (absolute figures).

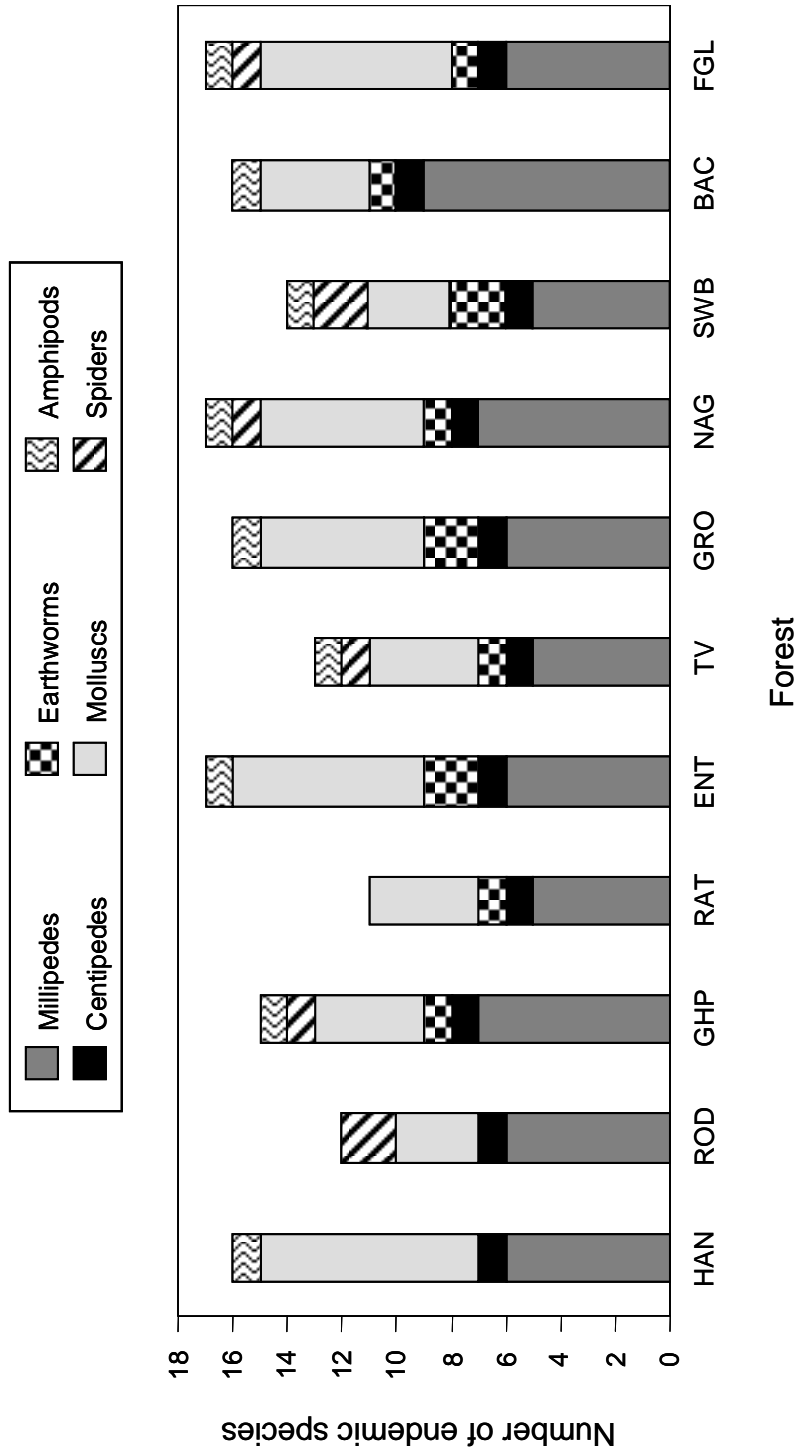


Figure 4.9: Taxon contributions to the total number of endemic species recorded in each forest. Numbers include site, local, regional and national endemics. Forest names are abbreviated as follows: Hanglip = HAN, Roodewal = ROD, Goedehoop = GHP, Ratombo = RAT, Entabeni = ENT, Thathe Vondo = TV, Grootbosch = GRO, New Agatha = NAG, Swartbos = SWB, Baccarat = BAC, Forest Glens = FGL.

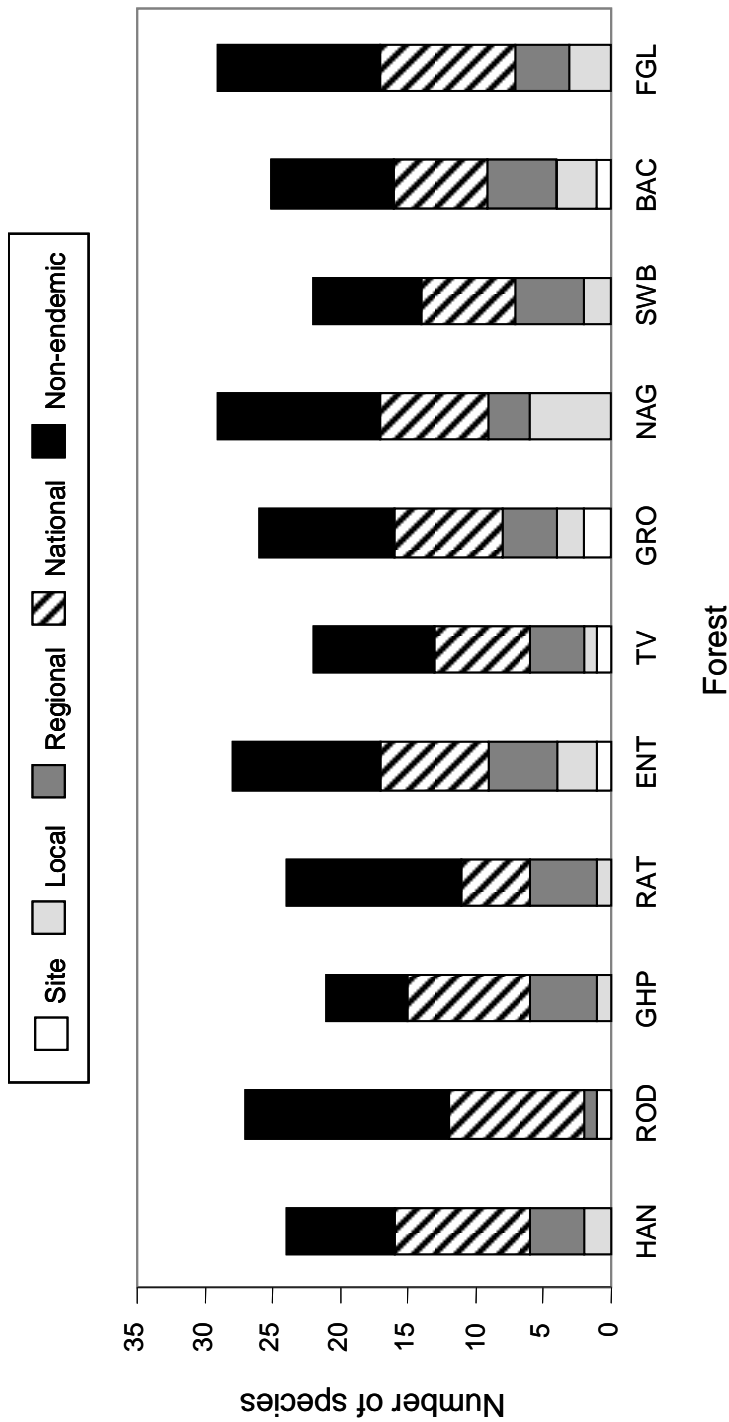


Figure 4.10: The numbers and levels of endemic species (for all target taxa) sampled in each forest, excluding introduced species and those species that could not be identified. Forest names are abbreviated as follows: Hanglip = HAN, Roodewal = ROD, Goedehoop = GHP, Ratombo = RAT, Entabeni = ENT, Thathe Vondo = TV, Grootbosch = GRO, New Agatha = NAG, Swartbos = SWB, Baccarat = BAC, Forest Glens = FGL.

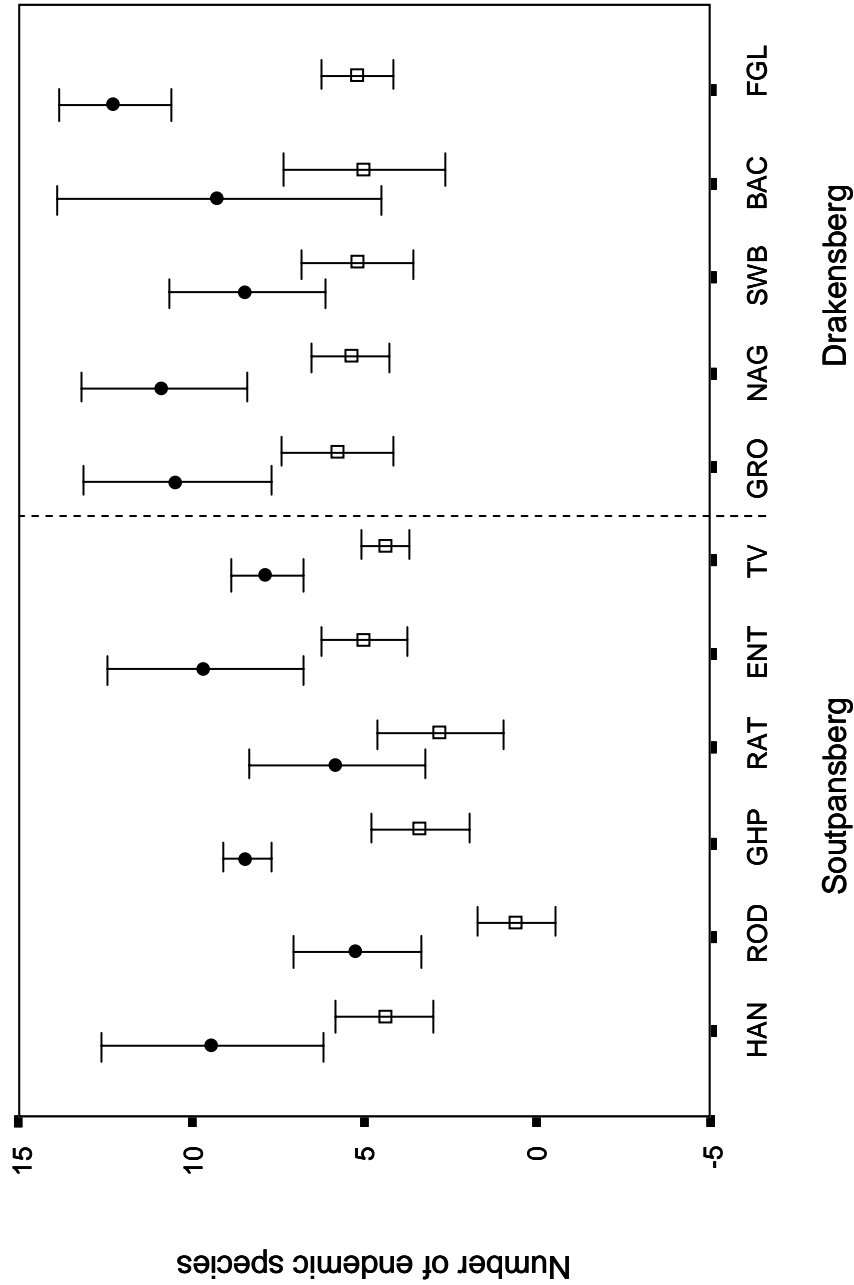


Figure 4.11: The number of endemics for each sampled forest, with the total endemics (all levels, ●), Limpopo Province forest endemics (regional, local and site levels, □) and 95% confidence limits. Forest names are abbreviated as follows: Hanglip = HAN, Roodewal = ROD, Goedehoop = GHP, Ratombo = RAT, Entabeni = ENT, Thathe Vondo = TV, Grootbosch = GRO, New Agatha = NAG, Swartbos = SWB, Baccarat = BAC, Forest Glens = FGL.

Table 4.2: Significant differences in numbers of endemic species between forests when all endemics (●) and Limpopo Province forest endemics (■) are considered, where $P < 0.05$ (post hoc test LSD). Shaded symbols indicate that the forest in the left column was higher and unshaded symbols indicate that the forest in the top row was higher. Forest names are abbreviated as follows: Hanglip = HAN, Roodewal = ROD, Goedehoop = GHP, Ratombo = RAT, Entabeni = ENT, Thathe Vondo = TV, Grootbosch = GRO, New Agatha = NAG, Swartbos = SWB, Baccarat = BAC, Forest Glens = FGL.

	HAN	ROD	GHP	RAT	ENT	TV	GRO	NAG	SWB	BAC	FGL
HAN											
ROD	○ □										
GHP		● ■									
RAT	○ □	■									
ENT		● ■	■	● ■							
TV		■		■							
GRO		● ■	■	● ■							
NAG		● ■	■	● ■		●					
SWB		● ■	■	■							
BAC		● ■	■	● ■							
FGL	●	● ■	● ■	● ■		●			●	●	

Linear regression analysis

Linear regression was used to determine if the distance from possible sites of forest refugia was related to the number of local and site endemic species in Limpopo Province forests. First, the relationship between forests' species richness and number of endemics was determined. Although there was no significant relationship, (Linear regression: $R^2 = 0.254$, $F_{1,10} = 3.069$, $P = 0.114$), the regression showed that Roodewal and Ratombo were outliers and that these two forests were on a different curve than the others (Figure 4.12). Roodewal and Ratombo were subsequently removed from this analysis.

After species richness, forest patch isolation and forest size were factored out using residuals, linear regression showed that there was a significant negative relationship between the distance from a site of forest refuge and the number of local and site endemics in forests (Figure 4.13). This trend was evident when either Ngome Forest (Linear regression: $R^2 = 0.601$, $F_{1,8} = 10.526$, $P = 0.014$, Figure 4.13a) or Mariepskop Forest (Linear regression: $R^2 = 0.568$, $F_{1,8} = 9.206$, $P = 0.019$, Figure 4.13b) was used as the site of forest refuge. The number of local and site endemics increased as the distance from a site of forest refuge decreased.

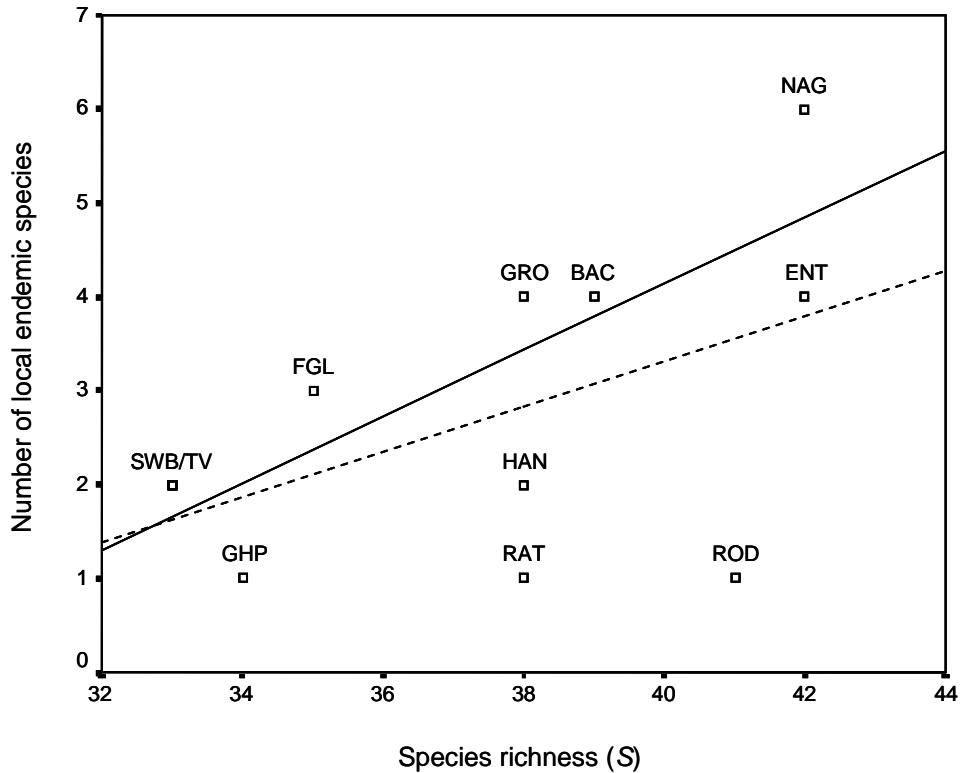


Figure 4.12: The relationship between species richness (S) and the number of local endemic species in Limpopo Province forests, with Roodewal and Ratombo included (dotted line) and without Roodewal and Ratombo (solid line). Forest names are abbreviated as follows: Hanglip = HAN, Roodewal = ROD, Goedehoop = GHP, Ratombo = RAT, Entabeni = ENT, Thathe Vondo = TV, Grootbosch = GRO, New Agatha = NAG, Swartbos = SWB, Baccarat = BAC, Forest Glens = FGL.

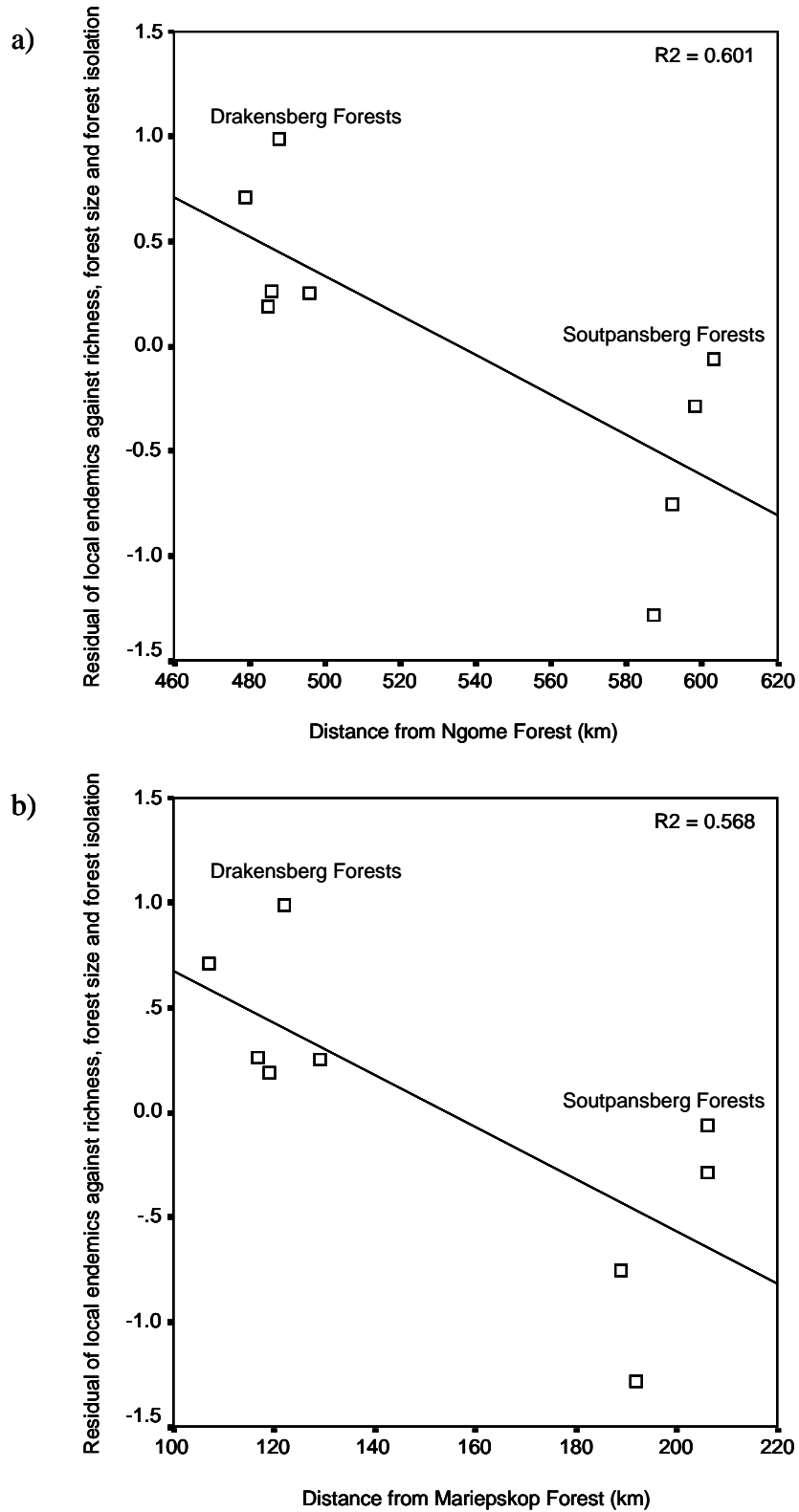


Figure 4.13: The relationship between the distance from site of forest refuge (connectively to regional species pool) and the number of local endemics in Limpopo Province forests, when a) Ngome Forest and b) Mariepskop Forest are used as forest refuge sites. Note that both relationships were significant.

4.3.4 Comparison with Zimbabwean and KwaZulu-Natal forests

Millipedes

Lists compiled from Hamer (1998) included 31 species from selected Zimbabwean forests (Appendix 11) and 41 species from selected KwaZulu-Natal forest localities (Appendix 12). The Soutpansberg list included 23 species (15 from the present study, eight from Hamer 1998) and the northern Drakensberg list comprised 15 species (13 from the present study, two from Hamer 1998).

The dendrogram generated shows that the Soutpansberg and northern Drakensberg were the most similar in terms of millipede genera. These Limpopo Province forests were then most similar to the forests of KwaZulu-Natal and the forests of Zimbabwe were the least similar to any other forested region (Figure 4.14).

The Jaccard similarity coefficients obtained revealed the same pattern and values ranged from 0.15 to 0.78 (Table 4.3). However, this analysis also showed that the Soutpansberg and northern Drakensberg forests were equally similar to the KwaZulu-Natal forests and to the forests of Zimbabwe. KwaZulu-Natal and Zimbabwean forests were the least similar in terms of millipede genera. Although Limpopo Province forests were most similar to KwaZulu-Natal forests, the coefficients also show that there was some similarity between the Limpopo Province and Zimbabwean forests.

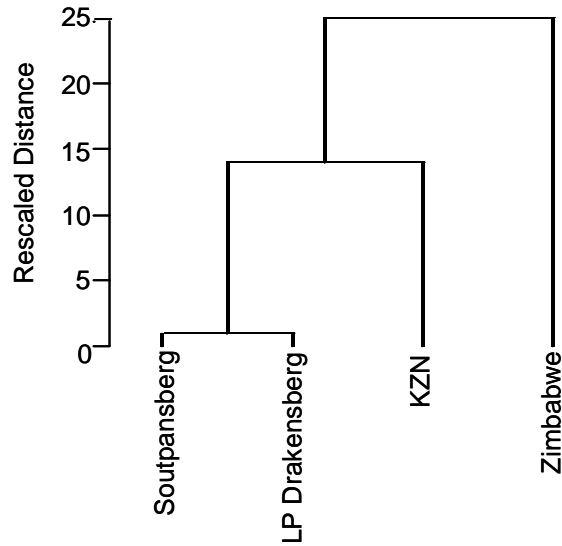


Figure 4.14: Dendrogram for millipede genera shared between regional forests using the average linkage between groups and Euclidean distances. The following abbreviations have been used: Zimbabwe = eastern highlands of Zimbabwe, KZN = KwaZulu-Natal and LP = Limpopo Province.

Table 4.3: Similarities in millipede genus composition between regional forests (Jaccard similarity coefficients). All values have been multiplied by 100 for ease of interpretation. The following abbreviations have been used: Zimbabwe = eastern highlands of Zimbabwe, KZN = KwaZulu-Natal and LP = Limpopo Province.

Site	Zimbabwe	KZN	Soutpansberg	LP Drakensberg
Zimbabwe	-			
KZN	15	-		
Soutpansberg	25	47	-	
LP Drakensberg	25	47	78	-

Molluscs

The list compiled from selected Zimbabwean forests includes a total of 35 mollusc species (Appendix 13) and the KwaZulu-Natal forest list includes 37 species (Appendix 14). After the previously recorded mollusc species were added, the Soutpansberg list comprised 37 species and the northern Drakensberg included 18 species.

Like the dendrogram for millipede genera, the dendrogram created for mollusc species shows that the Soutpansberg and northern Drakensberg were most similar in composition. The Limpopo Province forests were then most similar to KwaZulu-Natal forests, while Zimbabwean forests were the least similar to any other region (Figure 4.15a). The dendrogram for mollusc genera shows the same trend, except the similarity between Limpopo Province and KwaZulu-Natal forests is stronger at this level (Figure 4.15b).

The Jaccard similarity coefficients calculated for mollusc species and genera revealed the same general pattern as the dendrograms (Table 4.4). On the species level, the strongest similarity was found between the Soutpansberg and northern Drakensberg (Table 4.4a). However, on the genus levels of comparison, the strongest similarity was found between the Soutpansberg and KwaZulu-Natal, not the Soutpansberg and northern Drakensberg (Table 4.4b). Even on the species level, the Soutpansberg was more similar than the northern Drakensberg to KwaZulu-Natal. At both levels, Zimbabwean forests were the most dissimilar to other regions.

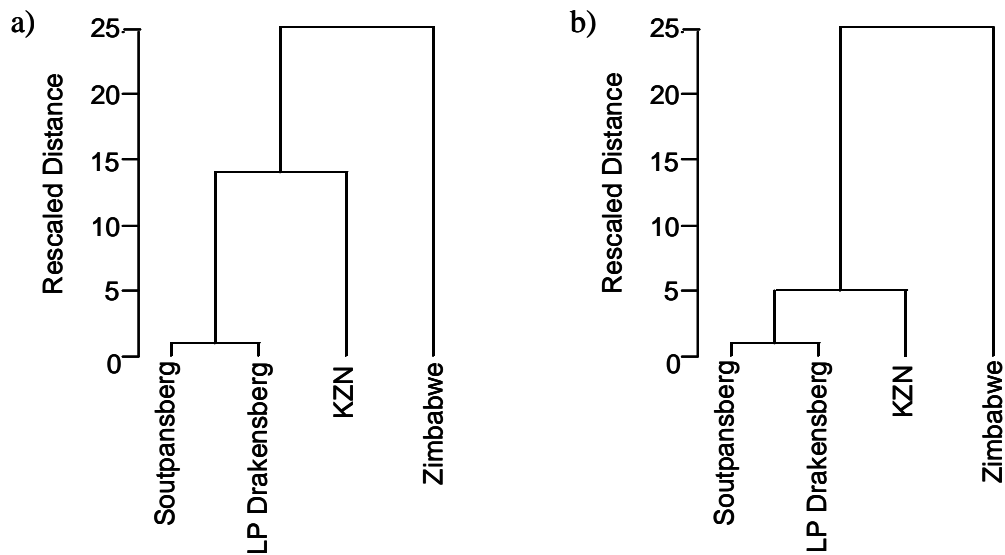


Figure 4.15: Dendrograms for mollusc a) species and b) genera shared between regional forests using the average linkage between groups and Euclidean distances. The following abbreviations have been used: Zimbabwe = eastern highlands of Zimbabwe, KZN = KwaZulu-Natal and LP = Limpopo Province.

Table 4.4: Similarities in mollusc a) species and b) genera composition between regional forests (Jaccard similarity coefficients). All values have been multiplied by 100 for ease of interpretation. The following abbreviations have been used: Zimbabwe = eastern highlands of Zimbabwe, KZN = KwaZulu-Natal and LP = Limpopo Province.

Site	Zimbabwe	KZN	Soutpansberg	LP Drakensberg
Zimbabwe	-			
KZN	3	-		
Soutpansberg	6	25	-	
LP Drakensberg	4	17	38	-

Site	Zimbabwe	KZN	Soutpansberg	LP Drakensberg
Zimbabwe	-			
KZN	16	-		
Soutpansberg	31	54	-	
LP Drakensberg	17	35	48	-

4.4 DISCUSSION

4.4.1 Site similarity

Although there were some variations according to target group, results generally emphasised similarities in forests' invertebrate species and family composition according to forest subtype (Table 4.1, Figures 4.4 and 4.5). The forest classification system followed during this study was largely derived from floristic data (von Maltitz *et al.* 2003), so patterns in invertebrate species composition generally correspond with those of plants. Similarities between forests' family compositions were stronger than for species because many families have wider distributions than most species.

Biogeographic theory would suggest that similarities in species composition should be most marked in forests relatively close to one another. A study by Geldenhuys (1989) has shown that southern African forests share many more floral species with their nearest neighbours than with forests further away. The Jaccard coefficients and dendrograms given in this chapter indicate that forests in the same region, thus closer forests, are generally more similar in species composition than are forests in different regions (Table 4.1, Figures 4.4 and 4.5).

This theory was also tested across forested archipelagos in Limpopo Province, where the Drakensberg forest patch closest to the Soutpansberg was expected to be most similar to that region and vice versa. The expected pattern was evident when the Drakensberg forests were compared to the Soutpansberg region. In terms of target invertebrate species, the Drakensberg forest patch closest to the Soutpansberg (i.e. Grootbosch) was most similar to that region and the Drakensberg forest patch furthest from the Soutpansberg (i.e. Forest Glens) was the least similar (Figure 4.3). However, this pattern did not hold true at the family level or when Soutpansberg forests were compared to the Drakensberg region. Nevertheless, when the semi-deciduous forest subtypes were removed from the analysis, a clear east to west gradient of decreasing similarity between the individual Soutpansberg forests and the Drakensberg region was seen. These results were surprising because expectations were based on the assumption that dispersal corridors between the regions are oriented directly north-south, which is the shortest possible distance between the regions. However, the results suggest that radiation from the Drakensberg to the Soutpansberg (or

from the Soutpansberg southward) occurred in corridors with more westerly orientations, linking the Drakensberg more closely to the western Soutpansberg forests (Figure 4.16). If this is indeed the case, Hanglip would be the sampled forest most closely linked to the Drakensberg and Thathe Vondo would be the most isolated from the region.

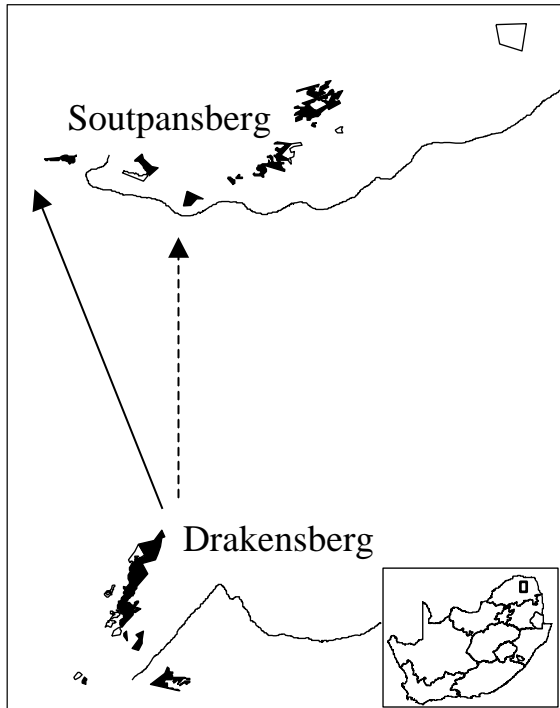


Figure 4.16: Two possible orientations of dispersal corridors between Drakensberg and Soutpansberg forests in Limpopo Province. The solid line indicates the orientation supported by the results of the present study. The dotted line indicates the shortest possible corridor.

4.4.2 Endemism

The degree of endemism in local faunas is arguably as important as their overall diversity (Hawksworth & Kalin-Arroyo 1995) and areas with high levels of endemism are more valued for conservation than those only supporting high species richness (Hamer & Slotow 2002). The Afromontane region of sub-Saharan Africa is considered a centre of endemism and about 75% of plants and 65% of birds recorded in the region are endemics (Huntley 1988). However, a large number of endemic plant species are widely distributed in the region and familiar and generic endemism are poorly developed (White 1978). On local and regional scales, tree endemism is low in the Afromontane region (Meadows & Linder 1989; Midgley *et al.* 1997).

Because of its geological history and geographical location, the Soutpansberg contains a disproportionately high diversity of organisms (Foord *et al.* 2002) and is considered to be a centre of botanical endemism within the southern African region (Hahn 1994). During their study of Limpopo Province forests, Geldenhuys and Venter (2002) sampled at least 17 plant species endemic to southern Africa, 35 plant species endemic to South Africa and 13 plant species endemic to Limpopo Province and Mpumalanga. They also identified several plant species that may be local endemics (Geldenhuys & Venter 2002). The present study has shown that there are also considerable numbers of invertebrate endemics in Limpopo Province forests (Figures 4.9 and 4.10). Endemics (all levels) accounted for 46% (47 species) of all identified target species and Limpopo Province forest endemics accounted for more than 22% (23 species) of all identified target species, including introduced species. In contrast, there are no locally endemic bird or mammal species (Forbes 2003) and there is only one frog species (*Breviceps sylvestris* FitzSimons, 1930, Carruthers 2001) endemic to Limpopo Province forests.

This study has shown that certain invertebrate target groups contain proportionately more endemics than others in Limpopo Province forests (Figure 4.6). This is probably due to differences in the dispersal abilities, rates of speciation and tolerances to environmental conditions between target groups. Groups with a high proportion of endemics, particularly those confined to forests at the regional, local and site levels (as defined in Section 4.2.3), were expected to have limited dispersal abilities, high rates of speciation, low tolerances to the environmental conditions outside of forests or a combination of these traits.

In Limpopo Province forests, earthworms had the highest proportion of endemics of all target groups (total of all levels, Figure 4.6). South African endemic earthworms, particularly the Acanthodrilidae, are known to be restricted to high rainfall areas (> 20 inches per year, Pickford 1937) and most earthworms cannot survive extended periods of desiccation (Lee 1985). With the exception of the ‘peregrine’ earthworm species that have been dispersed widely by man, the earthworms found in Limpopo Province forests are apparently poor dispersers, at least across the dry regions that separate forest archipelagos. However, there was only one site endemic, which suggests that most of the indigenous earthworm species sampled have been able to disperse across the shorter distances that separate individual forested patches. If introduced earthworms are also considered, the proportion of earthworm endemism in Limpopo Province forests drops to only 17%.

Millipedes, which had the second highest proportion of endemics (total of all levels, Figure 4.6), have limited powers of dispersal that have resulted in a high degree of speciation and a large number of species with very restricted ranges (Hopkin & Read 1992). Millipedes also have low tolerances to desiccation, so forest specialists are confined to forested areas (M. L. Hamer 2003, pers. comm.). Unlike earthworms, millipedes had a relatively high proportion of site endemics.

The lowest proportions of endemics occurred in the centipedes and spiders (Figure 4.6). Spiders, which are able to disperse easily across large distances due to their ability to suspend silk in air currents and ‘fly’ (Dippennar-Schoeman & Jocque 1997), were not expected to have high levels of endemism. In addition, spider sampling and species identification was the least successful of all the groups investigated (see pg. 133). However, such a low proportion of endemic centipedes was surprising, since they are similar to millipedes in mobility and habitat requirements. According to Hamer (2003, pers. comm.), such low levels of centipede endemism may be due to a number of factors, including a high tolerance of conditions outside of forests or taxonomic inaccuracies. Centipede taxonomy, even for the large, conspicuous scolopendromorphs, is plagued with numerous problems (Lewis 2003). If species are not properly described endemism figures for sampled species will certainly be incorrect. Unfortunately, we do not have enough knowledge of centipede taxonomy or biology to determine the reasons for these low endemism figures.

Because our knowledge of invertebrate taxonomy and distribution is generally poor (see Sections 1.1.4, 1.4), the endemism figures presented in this chapter cannot be considered definitive. Rather, the figures are based only upon the data that is currently available. As taxonomy is revised and more distribution data becomes available for southern African invertebrates, the categorisation of endemics in Limpopo Province forests may change.

To put Limpopo Province forest invertebrate endemism into perspective, numbers of endemics were compared with patterns of endemism in other areas and at other scales.

Millipedes

In southern Africa, most species of millipedes are restricted to small areas (Kraus 1978). According to Hamer & Slotow (2002), 89% of all South African millipede species are

endemic to the country. Results from this study show that the Limpopo Province forest millipedes follow the same pattern as the whole country's millipedes, with 90% of identified Limpopo Province forest millipede species endemic to South Africa (Figure 4.6). However, the amount of millipede endemism in Limpopo Province forests is not exceptional when compared to other forest areas. For example, Hoffman (1993) found that the great majority of millipede species and genera occurring in the Tanzanian Eastern Arc mountains are endemic to the immediate area. In the present study, only 48% of identified millipedes were Limpopo Province forest endemics (regional level, Figure 4.6), only 20% were site endemics (site level, Figure 4.6) and there were no endemic millipede genera found. Compared to other forested sites within South Africa, Limpopo Province forests do not support exceptional numbers of millipede endemics, but there are forests that contain lower numbers (Table 4.5).

Table 4.5: The numbers of site and national endemic millipedes in selected South African forested sites (from Hamer & Slotow 2002). Forests are listed in descending order of total millipede endemics. Because of differences between definitions, the local and regional levels could not be compared, but these numbers are included as national endemics.

<i>Site</i>	<i>Province</i>	<i>Number of site endemics</i>	<i>Number of national endemics</i>	<i>Total</i>
Kranskop	KwaZulu-Natal	5	18	23
Table Mountain, Cape Town	Western Cape	9	9	18
Pietermaritzburg, Town Bush	KwaZulu-Natal	8	9	17
Drakensberg, Champagne Castle	KwaZulu-Natal	4	13	17
Nkandhla Forest	KwaZulu-Natal	4	11	15
Tsitsikama	Eastern Cape	7	4	11
Mazongwaan Forest	KwaZulu-Natal	3	8	11
Drakensberg, Cathkin Peak	KwaZulu-Natal	0	11	11
Baccarat Forest (this study)	Limpopo	1	9	10
Ngome Forest	KwaZulu-Natal	5	4	9
Karkloof	KwaZulu-Natal	0	8	8

A large proportion of the endemic millipedes sampled in Limpopo Province forests belonged to the genera *Gnomeskelus* (39%) and *Sphaerotherium* (33%). The high level of endemism in *Gnomeskelus* was not surprising, since this genus is known to have radiated in South African forests and species commonly have site or local range restrictions within the country (Hamer & Slotow 2002). However, the high proportion of *Sphaerotherium*

endemism was unexpected, since this taxon is known for its richness (Hamer & Slotow 2002), but not necessary its endemism.

Molluscs

There are two mollusc families and 15 mollusc genera endemic to southern Africa (van Bruggen 1978). Herbert (1998) and van Bruggen (1978) estimate terrestrial mollusc species endemism in southern Africa to be about 90% of the known species. Results from the present study were considerably lower, since only about 54% of all identified mollusc species were classified as endemics (all levels, Figure 4.6). However, the present study did not consider the southern African subregion level and small (less than five millimetres) molluscs were not collected. About 19% of all identified mollusc species sampled in the present study were local or site endemics. These results are high when compared to studies such as Barker and Mayhill (1999), who found that only 2% (2 species) of terrestrial molluscs were endemic to northeastern New Zealand forests in the Pukeamaru Ecological District. However, in the African context the proportion of mollusc endemism in Limpopo Province forests is not remarkable. Emberton *et al.* (1997) found that 42% of mollusc species were endemic to a single forest site in eastern Tanzania and Tattersfield, Warui, Seddon & Kiringe (2001) found that 10% of molluscs were endemic to a single mountain, Mount Kenya. In the present study, only one mollusc site endemic was identified, *Chlamydephorus* sp. n.

Endemic molluscs (all levels) in Limpopo Province forests were mostly from the genera *Gulella* (40%) and *Trachycystis* (20%). This trend was not surprising because these genera are recognised for their high levels of endemism and explosive radiations in South Africa (Herbert 1998).

Spiders

Knowledge of the African spider fauna is largely restricted to taxonomy and ecological surveys of African spiders are particularly sparse (van der Merwe *et al.* 1996). Only five checklists have been compiled for spiders in conserved areas of South Africa (Foord *et al.* 2002). Current knowledge of Limpopo Province spiders is based only on short term collecting expeditions and only a single checklist has been published for the province's forests (western Soutpansberg, Foord *et al.* 2002). However, such checklists have given little or no attention to species endemism. Even texts written specifically on the

biogeography of southern African Arachnida have ignored endemism (i.e. Newlands 1978). Therefore, there is little information on patterns of spider endemism in South Africa and there is no comparative material.

Because spider sampling during this study was incomplete and focused only on selected habitats (see Section 3.4.1, Appendix 6), the figures for endemic spiders presented are likely to be underestimates. There were no site or local endemic spiders and the proportions of regional and national endemics were low (Figure 4.6). However, over 61% of all spider species sampled during this study could not be named (Appendix 1), so additional endemics may occur in the study area. Our knowledge of identification and distribution is simply too poor to determine the true figures. Each of the seven endemic (all levels) spiders identified in the present study was from a different genus and family so there were no patterns of endemism within spider taxa.

Other target groups

The proportion and amount of centipede endemism in Limpopo Province forests was low at all levels, at least compared to the other invertebrate target groups sampled (Figures 4.6 and 4.9). However, no comparative data could be found to determine if this degree of endemism is unusual by South African terms. The indigenous earthworm fauna of South Africa is known to have a high degree of local endemism (Pickford 1937). As expected, all earthworm species sampled during this study were classified as endemics (site to regional levels, Figure 4.6). Two genera accounted for all endemic earthworm species sampled in the Limpopo Province forests, *Parachilota* and *Tritogenia*. Both genera are endemic to South Africa (Pickford 1937; Plisko 1997). The single amphipod species sampled in the present study was a national endemic (Figure 4.6). In fact, most species of terrestrial amphipods are local endemics (Bousfield 1984) and all species that occur in South Africa are at least national endemics (Griffiths 1999). Because little or no published data exist on the amount of earthworm or amphipod endemism within other South African sites, comparative analyses cannot be presented.

4.4.3 Forest history and invertebrate distribution

Studies linking Limpopo Province forest history with species composition and distribution have suggested that assemblages are primarily the product of northward faunal radiations

from Pleistocene forest refugia and that the dry Limpopo River valley has been a significant barrier to the southward movement of species from tropical Africa. These trends have been found in forest amphibian (Poynton 1989; Forbes 2003), mammal (Lawes 1990) and bird (Clancey 1975; Symes *et al.* 2000; Forbes 2003) communities. This study has shown that Limpopo Province forest millipede and mollusc faunas are more closely linked to KwaZulu-Natal forests in the south than to the forests of the eastern highlands of Zimbabwe to the north (Figures 4.14 and 4.15, Tables 4.3 and 4.4). However, Limpopo Province forest communities are not simply subsets of more southern assemblages. They support a certain component of unique species, including site, local and regional endemics (this chapter), and similarity between Limpopo Province and KwaZulu-Natal forests is not 100%. This trend can be explained by two possible hypotheses: (1) forests in Limpopo Province completely disappeared during the last hypothermal and species from southern forest refugia radiated into these forests to comprise the major proportion of contemporary faunas or (2) small forest refugia remained in Limpopo Province where species did persist, but assemblages in contemporary forests have been augmented by species radiating from southern forest refugia.

Similarity analyses showed that there were some unique similarities between Limpopo Province and Zimbabwean forests. As a result, this study questions the effectiveness of the arid Limpopo River valley radiation barrier, even for animals with limited mobility and dispersal abilities. One sampled millipede species, *Centrobolus inyanganus* (Lawrence, 1967), has been recorded only from Soutpansberg and eastern Zimbabwean forest localities (Hamer 1998).

According to Huntley (1988), Pleistocene refugia are sites of contemporary species richness and endemism. Based solely on endemism data presented in this chapter, the Drakensberg is more likely to have contained refugia than the Soutpansberg, if forests remained in Limpopo Province during the Pleistocene at all. This is because the Drakensberg supports significantly more endemic invertebrate forest species in its mistbelt forests than the Soutpansberg.

Linear regression was used to determine if the distance from sites of Pleistocene forest refugia was related to the number of local endemics in Limpopo Province forests. But first, the relationship between site richness and number of local endemics was established.

Although it was not significant, the positive relationship between endemism and richness was not surprising (Figure 4.12), since landscapes with high numbers of endemics are often species-rich and a correlation between species richness and degree of endemism is evident in some cases (Hawksworth & Kalin-Arroyo 1995). Because endemism is often the product of habitat isolation (Hawksworth & Kalin-Arroyo 1995) and forest patch size may influence both richness and isolation, these variables were factored out of the regression.

The regression results show that forests located further away from Pleistocene refuge sites (i.e. the Soutpansberg forests) support less local target group endemics than closer forests (i.e. the northern Drakensberg forests) and this relationship was significant (Figure 4.13). Assuming that all Limpopo Province forests disappeared during the last hypothermal, species radiations would have reached the Limpopo Province Drakensberg before the more isolated Soutpansberg. As a result, the Drakensberg faunas would be older, species could be more specialized and endemism more developed. In this case, isolation would not promote endemism, contrary to the popular notion. This would also mean that the endemic species in the Soutpansberg should have close relatives in the Limpopo Province Drakensberg and that they will have speciated only in the last 16 000 years. These results suggest that historical processes are an important influence on local endemism in Limpopo Province forests.

4.5 CONCLUSION

Several analyses of Limpopo Province target invertebrate species distributions' were presented in this chapter and some important similarities were found between the species compositions of sites. However, each mountain region, forest vegetation subtype and forest patch contain unique invertebrate species. Limpopo Province forests support high numbers of endemic invertebrates, although the numbers and scales of endemism varied by target group. The northern Drakensberg had significantly more endemic invertebrate species (all levels and Limpopo Province forest endemics) than the Soutpansberg and mistbelt forests had significantly more endemic invertebrate species (all levels and Limpopo Province forest endemics) than semi-deciduous scrub forests and semi-deciduous

mixed forests. In addition, some forests contained significantly more endemics than others did. This information could prove useful in assigning conservation priorities.

Invertebrate species' distributions in Limpopo Province forests generally support the biogeographic theories of Pleistocene refugia and the Limpopo River valley as a radiation barrier, although some important contradictions were found. The linear regression analysis suggests that local endemism in Limpopo Province forests could be the product of historical processes.

Unlike the species richness, diversity and evenness values given in Chapter 3, the beta diversity measures and biodiversity patterns presented in this chapter consider the identities of species when comparing communities. Along with an understanding of some of the processes that influence species' distributions, they are more useful tools in conservation and habitat management.

CHAPTER 5

ASSESSMENT OF BIODIVERSITY SURROGATES

5.1 INTRODUCTION

Because the world's biodiversity is severely threatened, biodiversity conservation is currently one of the most important challenges facing humanity (Chapter 1). Yet meaningful conservation cannot take place if the species involved are not known (Foord *et al.* 2002). Species inventorying is the approach commonly used to identify, quantify and map species and to provide the baseline information necessary for the assessment of communities, prioritisation of areas for conservation and the monitoring of environmental change (Stork & Samways 1995). However, the vast diversity of natural systems, coupled with the pace at which humans are altering them, prevents biologists from cataloguing the identities and distributions of all species before conservation decisions must be made (Ehrich & Wilson 1991). According to Moore (1991), the risk of doing the wrong thing through lack of scientific knowledge is much less than the risk of delay.

In the absence of complete species inventories, several 'short cut' surrogacy or substitute methods have been developed, all of which aim to rapidly, inexpensively and accurately assess biodiversity or changes in communities. Surrogacy, according to Purvis & Hector (2000), is 'a pragmatic response to the frightening ignorance about what is out there.' The most common method of surrogacy is the use of bioindicators (biological indicators), readily measured biotic components that are used to provide information about the complex ecosystems in which they occur, and as such play key roles in conservation planning and management (Andersen 1999). McGeoch (1998) identified three classes of bioindicators that correspond to the main applications: (1) *environmental indicators*, taxa that are used to gauge disturbance or environmental change; (2) *ecological indicators*, which are used to demonstrate the effects of environmental change on biotic systems and (3) *biodiversity indicators*, taxa that are used to reflect some measure of the diversity of other taxa in a habitat. Only biodiversity indicators are addressed in this chapter.

Although vertebrates and plants are commonly used as bioindicators (Landres *et al.* 1988; Araujo 1999; Hilty & Merenlender 2000; Margules & Pressey 2000), many invertebrate taxa have been suggested as environmental, ecological or biodiversity indicators. Table 5.1 lists some of the suggested invertebrate taxa.

Table 5.1: Some suggested invertebrate bioindicators.

<i>Suggested invertebrate taxa</i>	<i>Class of bioindicator</i>	<i>Reference</i>
All insects	Biodiversity	Moritz <i>et al.</i> 2001
Ants	Ecological	Majer 1983; Andersen 1990
Ants	Environmental	Fabricius <i>et al.</i> 2003
Bees & wasps	Environmental & biodiversity	Brown 1991
Butterflies	Biodiversity	Beccaloni & Gaston 1995; Daily & Ehrlich 1995; Blair 1999
Butterflies	Ecological	Kremen 1992; Pollard & Yates 1993
Butterflies	Environmental & biodiversity	Erhardt & Thomas 1991
Butterflies & moths	Environmental & biodiversity	Brown 1991
Cicadas	Ecological	Milton & Dean 1992
Dragonflies	Environmental	Clark & Samways 1996
Dung beetles	Environmental	van Rensberg <i>et al.</i> 1999
Earthworms	Ecological	Paoletti 1999
Earthworms	Environmental	Xiaoming & Grizelle 1995
Flies	Ecological	Parsons 1991
Grasshoppers	Ecological	Fischer <i>et al.</i> 1997; Samways 1997
Ground beetles	Ecological	Stork 1990
Moths	Environmental	McGeoch & Chown 1997; Grout 1998
Spiders	Biodiversity	Schwab <i>et al.</i> 2002
Spiders	Ecological	Klimes 1987; Churchill 1997
Spiders	Environmental	Marc <i>et al.</i> 1999; Fabricius <i>et al.</i> 2003
Springtails	Ecological	Greenslade & Greenslade 1987
Springtails	Environmental & biodiversity	Brown 1991
Termites	Environmental & biodiversity	Brown 1991
Terrestrial molluscs	Biodiversity	Moritz <i>et al.</i> 2001
Tiger beetles	Biodiversity	Pearson & Carroll 1998
Tiger beetles	Ecological	Rodriguez <i>et al.</i> 1998
Tiger beetles	Environmental & biodiversity	Pearson & Cassola 1992
True bugs	Biodiversity	Schwab <i>et al.</i> 2002
Weevils	Environmental	Fabricius <i>et al.</i> 2003

5.1.1 Biodiversity indicators and invertebrate studies

Biodiversity indicators are easily measured, correlating subsets of total biodiversity (Gaston & Spicer 1998) that are used to suggest the extent and patterns of diversity in the larger group of interest. Because they promote efficiency, biodiversity indicators are particularly useful in assessing invertebrate communities, which are often perceived to be too time consuming, costly and difficult to include in species inventories (Oliver & Beattie 1993). This is because (1) invertebrates are diverse and it is impossible to compile complete species lists for almost all invertebrate groups on any broad scale; (2) many species are difficult to identify and most species identifications can only be made or confirmed by specialists; (3) there is considerable taxonomic uncertainty and many invertebrates are undescribed or have been described from a single site or from very few individuals; (4) taxonomic expertise is limited and may not exist for some taxa; (5) the diversity and distributions of species are largely unknown; (6) many invertebrates require specialized collecting techniques and (7) collection and identification of invertebrates is usually time consuming and relatively expensive (New 1998; Slotow & Hamer 2000). Clearly, biodiversity indicators offer a potential method of circumventing these problems, which would allow invertebrates to be more widely incorporated into inventories and conservation planning.

There are three main types of biodiversity indicators: (1) *indicator taxa*, individual species or taxa that are surveyed in place of entire faunas and are chosen to reflect the diversity of a much larger suite of taxa (Hammond 1995; Oliver & Beattie 1996a; McGeoch 1998; Slotow & Hamer 2000); (2) *higher taxa* methods that use other levels of identification in place of species (Balmford *et al.* 1996; Gaston & Spicer 1998) and (3) *morphospecies inventories* that are generated by non-specialists and are used in place of formal species inventories (Oliver & Beattie 1996a). All three of these biodiversity indicator types are investigated in this chapter.

Individual taxa as indicators of species richness

Because our current knowledge of invertebrate taxonomy and distribution is so poor, better known indicator groups must be used as surrogates for other taxa or total invertebrate diversity. The multi-taxa focal group approach, used throughout this study and discussed

in Section 2.1.3, is one such example. Alternatively, a single taxon can be used (McGeoch 1998). For example, the species richness of an individual indicator taxon can be used to estimate the species richness of other closely related taxa (Gaston & Blackburn 1995).

No single species or taxon can adequately represent or indicate patterns of diversity for all other species and taxa (Pearson 1994). Therefore, individual biodiversity indicator groups must be chosen carefully. In order to maximize their generality and success, several criteria have been suggested for the selection of individual biodiversity indicators: (1) ease, reliability and cost efficiency of sampling, sorting and identification; (2) available taxonomic expertise; (3) high abundance and diversity; (4) correlation with the larger group of interest; (5) trophic level representation, functional importance and habitat specialization; (6) sufficient knowledge of biology and life history and (7) wide geographical range (Landres *et al.* 1988; Hammond 1995; McGeoch 1998; New 1998; Andersen 1999; Caro & O'Doherty 1999). Each of the three classes of bioindicators has a different selection profile (Caro & O'Doherty 1999) and separate criteria have been given for environmental and ecological indicators (see Landres *et al.*; McGeoch 1998).

Many invertebrate taxa have been suggested as biodiversity indicators (Table 5.1), but there are alternatives to using a single invertebrate taxon. For example, invertebrates can be excluded entirely and inventorying and conservation area selection can depend entirely upon data for plants and/or vertebrates (Oliver & Beattie 1996b; Oliver *et al.* 1998). Plants and vertebrates are commonly used as indicators of total biodiversity, since data on these groups are easier to obtain than comparable invertebrate data (Mittermeier *et al.* 1998), especially on the global level. Birds, for example, are among some of the best-recorded organisms and are one of the most highly valued biotic groups (Williams *et al.* 1996). Plants, specifically angiosperms, are the group most commonly recorded in biodiversity studies (Schwab *et al.* 2002). Myers (1988; 1990) and Mittermeier *et al.* (1998) used plants as indicators of total biodiversity and for the identification of global biodiversity hotspots. Scott *et al.* (1993) also suggests that plant species diversity is a good indicator of overall biodiversity. According to Panzer & Schwartz (1998), plants rank among the most promising of all indicator taxa examined thus far.

The principle debate in the use of biodiversity indicators is whether the presence of any single taxon can signify the presence of other taxa to the extent that it can be considered a

suitable surrogate for overall biodiversity (Margules & Pressey 2000). The underlying value of any indicator taxon depends upon its predictive ability, as determined by the relationships or responses that it demonstrates (McGeoch 1998; Andersen 1999). One way of assessing the value of potential biodiversity indicator taxa is to quantify the degree to which patterns of species richness coincide across different taxa (Prendergast *et al.* 1993; Lombard 1995). Specifically, the richness of any biodiversity indicator must be positively correlated to the richness of the larger suite of taxa (Hammond 1995). In this chapter, I assess each individual invertebrate target group (millipedes, centipedes, earthworms, molluscs and spiders), birds and plants as potential indicators of ground dwelling, flightless invertebrate diversity in Limpopo Province forests. To do this, I determine if the richness of any individual invertebrate target group, birds or plants was correlated to total target invertebrate species richness. I also use correlations between individual taxon richness to assess if any group could be considered as a diversity indicator for any other group.

Higher taxa as indicators of species richness

It has been recognized that changes or differences in communities at the species level may also be evident at higher taxonomic levels such as genus or even phylum (Pik *et al.* 1999). As a result, higher taxa richness has been proposed as a surrogate for species richness and recent studies have found some success with this approach in both contemporary biota and fossils (Gaston & Williams 1993; Gaston & Blackburn 1995; Balmford *et al.* 1996; New 1998; Pik *et al.* 1999). The higher taxon approach is well established in aquatic pollution assessment and monitoring studies using benthic communities (Pik *et al.* 1999). Studies have shown that lower taxonomic level identification does not always improve the resolution of results obtained using higher taxonomic levels (Oliver & Beattie 1996a).

The use of higher taxa surrogates has been advocated largely because it overcomes the problems associated with species identification. This is particularly important when inventorying the richness of invertebrates or other speciose and poorly known groups. Using this approach, there are little or no costs for expert assistance in specimen identification, the challenges associated with a lack of taxonomic expertise are mostly eliminated and sorting is generally less labour intensive and time consuming (McGeoch 1998; Pik *et al.* 1999). The identities and distributions of higher taxa also tend to be better known than species (Gaston *et al.* 1995). In addition, there are no large numbers of species

to identify so a greater range of major taxa and functional relationships can be incorporated into surveys (Oliver & Beattie 1996a; McGeoch 1998).

Despite the advantages, this approach should be used with caution, since there are cases where higher taxa are not indicative of species numbers (Gaston & Spicer 1998). This surrogacy method requires good evidence that differences in species richness are mirrored at other taxonomic levels (Balmford *et al.* 1996). If they are not, the diversity estimates obtained may be misleading. In addition, higher levels of identification may cause a loss of information and interpretation sensitivity and decrease the comparability of results, since many families and orders are widespread and diverse (New 1998). Further, evidence justifying this approach comes mostly from temperate datasets or inventories over large areas and there are concerns about using this method in tropical areas (Balmford *et al.* 1996). In addition, few studies have been conducted using this method with terrestrial invertebrate assemblages (Pik *et al.* 1999). Prance (1994) suggests that species may be far better indicators of total diversity than higher taxa.

In this chapter, I assess the genus and family levels as indicators of target group invertebrate species richness by determining any relationship between species richness and higher taxon richness and establishing the relative accuracy of the genus and family levels as indicators of species richness.

Morphospecies as indicators of formal (true) species richness

The use of morphospecies is another recent attempt to improve the efficiency of biodiversity assessments. Instead of formal species, specimens are sorted by non-specialists to recognizable taxonomic units (RTUs) based solely on morphological characteristics (Hammond 1995; Oliver & Beattie 1996a; New 1998). In some cases, this approach has been useful and has produced richness estimates similar to those of formal species (Oliver & Beattie 1993; Oliver & Beattie 1996a; Pik *et al.* 1999).

Like the higher taxon method, the advantages to using morphospecies are mainly due to the avoidance of formal species identification. Because specimens do not require intense specialist taxonomic treatment, this method is less costly, is labour and time efficient and more taxa can be incorporated into surveys (Oliver & Beattie 1996a). However, there are also drawbacks to using this method. The legitimacy of morphospecies identification is

questionable, no distribution, endemism or interaction information can be extracted from the results and reliable comparisons cannot be made between communities (Slotow & Hamer 2000). The disadvantages associated with using morphospecies are discussed in more detail in Section 2.1.2.

The accuracy of morphospecies as a surrogate depends upon how closely the RTUs conform to true species and the degree of success clearly varies according to taxonomic group and the abilities of the sorters (Hammond 1995). Sorting errors are the consequence of using non-specialists and diversity can be under- or overestimated by lumping or splitting true species into morphospecies (New 1998; Pik *et al.* 1999). Underestimation can result when formal species appear alike superficially and are only classified by minute or internal structures (New 1998; Slotow & Hamer 2000). Overestimation can occur with polymorphic species or when individuals of the same species appear different because of sex, age or developmental stage (New 1998; Slotow & Hamer 2000).

Formal species identification has been used throughout this study. However, in this chapter I evaluate invertebrate morphospecies as an indicator of true invertebrate species richness by comparing the total morphospecies richness to total formal species richness. Invertebrate target groups were also evaluated individually to establish the relative accuracy of morphospecies identification for each taxon.

5.1.2 Land classes as surrogates for species' distributions

Biodiversity indicators rely upon biotic data (usually species) to signify patterns of diversity. However, there are problems associated with species data in conservation planning. Species data obtained from museums and herbariums are notoriously biased, having been collected for a different purpose, and often in an opportunistic manner from easily accessible areas (Nelson *et al.* 1990; Hamer & Slotow 2002). In addition, these data are often not quantified. Species data are usually incomplete due to inadequate coverage of areas and records tend to be biased towards species that are easy to observe or collect or whose taxonomy is well established (Belbin 1993; Haila & Margules 1996). Further, most species data only represent presence; there are few data for where species do not occur, although this absence information is crucial for spatial modelling (Nicholls 1991).

As a potential solution to these problems, some studies have used remotely derived environmental data as surrogates for species' distributions in the selection of areas for conservation (Faith *et al.* 2001). Abiotic information such as climate, topography and nutrients have been used to identify significant factors that control the distribution of biota (Belbin 1993) and are used to describe landscapes and to classify land areas. These environmental variables are simpler and cheaper to sample than the biota, especially on regional or national scales, and are often the only option in understudied areas (Belbin 1993; Margules & Pressey 2000; Faith *et al.* 2001). Environmental surrogates are usually discrete land classes, but can also be continuous variables (Lombard *et al.* 2003). Although biological precision is lost, land classes based upon environmental data provide spatial consistency across wide areas and can integrate more of the ecological processes that contribute to ecosystem maintenance into conservation (Margules & Pressey 2000).

The environmental method of surrogacy and conservation prioritisation, sometimes called the 'habitat approach,' uses abiotic data to identify representative networks of land systems or environmental domains that themselves are used as surrogates for biodiversity (Mackey *et al.* 1989; Belbin 1993). The goal is to conserve the diversity of habitats in a landscape, with the assumption that the subset of sites chosen will represent most species within that area and that species diversity in many taxa will be conserved (Oliver *et al.* 1998; Ricketts *et al.* 2002).

Because they attempt to predict the species composition of an area based on its abiotic classification, environmental surrogates are only valuable if land classes are truly representative of species (Araujo *et al.* 2001). This can be determined only if species' distributions within and between land classes are known (Lombard *et al.* 2003). In addition, surrogacy is only successful if each class has characteristic species assemblages (York 1999) and if there is consistency of species' compositions within each specific land class. However, these conditions remain largely untested (York 1999) and species may be patchily distributed due to high levels of endemism, high turnover along gradients or historical factors (Lombard *et al.* 2003). Studies have shown that broadly defined land classes based upon environmental data can overlook species, particularly those with narrow distributions, and even miss entire habitats (Araujo *et al.* 2001; Reyers *et al.* 2002). To address this problem, species data are sometimes incorporated into land classes. This can be achieved by (1) targeting land classes and available species data simultaneously or

(2) redefining land classes to reflect biological heterogeneity and gradients of biological distinctiveness (Lombard *et al.* 2003, Ferrier 2002).

Vegetation classification in South Africa has a long history of integrating species into land classes. The earliest forest classifications, proposed by Laughton (1937) and Robertson (1924), were based upon the amount and quality of merchantable timber species. More recent vegetation classifications have used floral communities as primary criteria for categorization (Rutherford & Westfall 1994; Low & Rebelo 1996). The land classes used in this study were those proposed by von Maltitz *et al.* (2003) which incorporate environmental data (climate and soils) and plant, bird, mammal, frog and reptile species into land classes.

In this chapter, I determine if forest subtype can be used as a surrogate for the target group invertebrate species distributions in Limpopo Province forests. That is, can forest subtype predict the invertebrate composition of forests?

Biodiversity indicators, including individual taxa, higher taxa and morphospecies, and land classification systems are commonly used to identify areas of conservation priority to aid in reserve selection and conservation planning. In this chapter, I determine if any of these surrogate methods could be used to direct invertebrate conservation efforts in Limpopo Province forests by assessing how accurately they reflect the true species richness of target invertebrates.

5.2 METHODS

Invertebrates from the seven target taxa were sampled according to the three sampling methods in 11 forest patches in Limpopo Province as described in Chapter 2. The indigenous species obtained in these samples were included in the following analyses. All of the analyses in this chapter were performed using the statistical program SPSS (Norusis 1994).

5.2.1 Individual taxa as indicators of species richness

All target group invertebrates sampled were formally identified by specialists. In most cases, invertebrates could be identified to the species level. The cumulative species richness (S) of Limpopo Province forests was calculated for each target group and for all target groups combined (total target species richness). Because only one species of amphipod and one scorpion species were sampled, these groups were only included in this analysis as part of the total species richness. The plant species richness of each forest sampled was obtained from Geldenhuys & Venter (2002). The richness of birds in eight forests (Hanglip, Ratombo, Entabeni, Thathe Vondo, Grootbosch, Swartbos, Baccarat and Forest Glens) was obtained from Forbes (2003). Because bird richness data were not available for New Agatha, Goedehoop and Roodewal, these forests were excluded from all analyses that included birds.

First, data collected in each forest sampled were used to assess if any individual taxon could be used to indicate total target group species richness in Limpopo Province forests. Using linear regression and Pearson's correlation coefficients, the relationship between total target invertebrate species richness and the species richness of each of the five major invertebrate target groups (millipedes, centipedes, earthworms, molluscs and spiders), plants and birds was determined. The strength of each relationship was determined by the value of the R^2 and correlation coefficient.

Second, data from individual forests were used to determine if any taxon could accurately indicate the richness of any other taxon. Using linear regression and Pearson's correlation coefficients, the relationship between each pair of individual taxa (including target invertebrate groups, plants and birds) was determined. The strength of each relationship was determined by the value of the R^2 and correlation coefficient.

5.2.2 Higher taxa as indicators of invertebrate species richness

Target invertebrates sampled in Limpopo Province forests were identified to the family, genus and species levels by specialists. The cumulative total family, genus and species richness were calculated for all indigenous target invertebrates sampled with quantified methods in Limpopo Province forests. Linear regression and Pearson's correlation

coefficients were then used to determine the relationships between total invertebrate family, genera and species richness. The strengths of the relationships were then compared using the R^2 values and Pearson's correlation coefficients. To simulate a possible conservation application of higher taxon calculations, all forests were ranked in order of decreasing species, genera and family richness.

5.2.3 Morphospecies as indicators of formal (true) invertebrate species richness

Target invertebrates were sampled using three quantified methods as detailed in Chapter 2. One sampling method, the pitfall traps, also captured a considerable number of ants.

All specimens were sorted in the field laboratory to morphospecies by J. Horn and training prior to sorting was minimal for all groups. Morphospecies were sorted following the protocols of Oliver and Beattie (1993) and Beattie and Oliver (1994) using external morphology only and without the use of keys. The cumulative morphospecies richness was calculated for each group sampled, including non-target groups. Upon completion of the field work, specimens were sent to specialists for formal species identification (Section 2.4.6). Because they could be reliably identified to species level, the following groups were included in this analysis: millipedes, centipedes, earthworms, molluscs, spiders, amphipods and ants. Using only these groups, the total morphospecies richness and total true species richness were calculated using simple counts (S). Both indigenous and exotic species were considered here, since this information was not available when sorting morphospecies.

First, a one way ANOVA was used to identify the significance of differences between the total invertebrate morphospecies and total true species richness sampled in forests and between the morphospecies and true species richness of each group. Amphipods were excluded from this part of the analysis because only one species of amphipod was sampled. A Kolmogorov-Smirnov goodness of fit test was used to determine the normality of the data distribution.

Second, the relationship between total invertebrate morphospecies and true species richness and between the morphospecies and true species richness of each group was

determined using linear regression and Pearson's correlation coefficients. The strength of each relationship was determined by the value of the R^2 and correlation coefficient.

5.2.4 Vegetation classification as a surrogate for invertebrate species' distributions

Each forest sampled was classified according to von Maltitz *et al.* (2003) as one of three forest subtypes. All forests were the mistbelt subtype, except Roodewal (semi-deciduous scrub) and Ratombo (semi-deciduous mixed).

To assess if forest subtype could be used to indicate the species composition of forests, some of the results presented in Chapter 4 were reevaluated, particularly the results shown in Figures 4.1a (pg. 106) and 4.4a (pg. 110), and Table 4.1a (pg. 105).

5.3 RESULTS

5.3.1 Individual taxa as indicators of species richness

There were no significant relationships between the species richness of individual invertebrate target groups, plants and birds and the total target invertebrate species richness (all $P > 0.05$, Table 5.2, Figures 5.1 and 5.2). Therefore, there was no evidence to support the use of any single taxon to indicate the richness of target invertebrates in Limpopo Province forests. Although no relationship was significant, the strongest relationship was between bird richness and total target invertebrate species richness (Table 5.2 and Figure 5.2). The weakest relationship was between earthworm richness and total target invertebrate species richness (Table 5.2 and Figure 5.1).

There were also no significant relationships between the species richness of individual target invertebrate groups, plants and birds (all $P > 0.05$, Table 5.3), except between millipedes and centipedes (Linear regression: $R^2 = 0.531$, $F_{1,10} = 10.200$, $P = 0.011$, Figure 5.3). Thus, centipede richness could be used to indicate the richness of millipedes in Limpopo Province forests (or vice versa), but other groups cannot be used in this way. After millipedes and centipedes, the strongest relationship was between bird richness and

centipede richness and the weakest relationship was between millipede richness and earthworm richness (Table 5.3).

Table 5.2: Summary of the relationships between total target invertebrate species richness (total S) and the richness (S) of each taxon investigated. Note that there were no significant relationships.

	Linear Regression R^2	Linear Regression $F_{1,10}$	Pearson's coefficient	P
Total S vs millipede S	0.231	2.699	0.480	0.135
Total S vs centipede S	0.218	2.508	0.467	0.148
Total S vs earthworm S	0.005	0.047	0.072	0.833
Total S vs mollusc S	0.218	2.507	0.467	0.148
Total S vs spider S	0.047	0.441	0.216	0.523
Total S vs plant S	0.118	1.204	0.344	0.301
Total S vs bird S	0.286	2.402	0.535	0.172

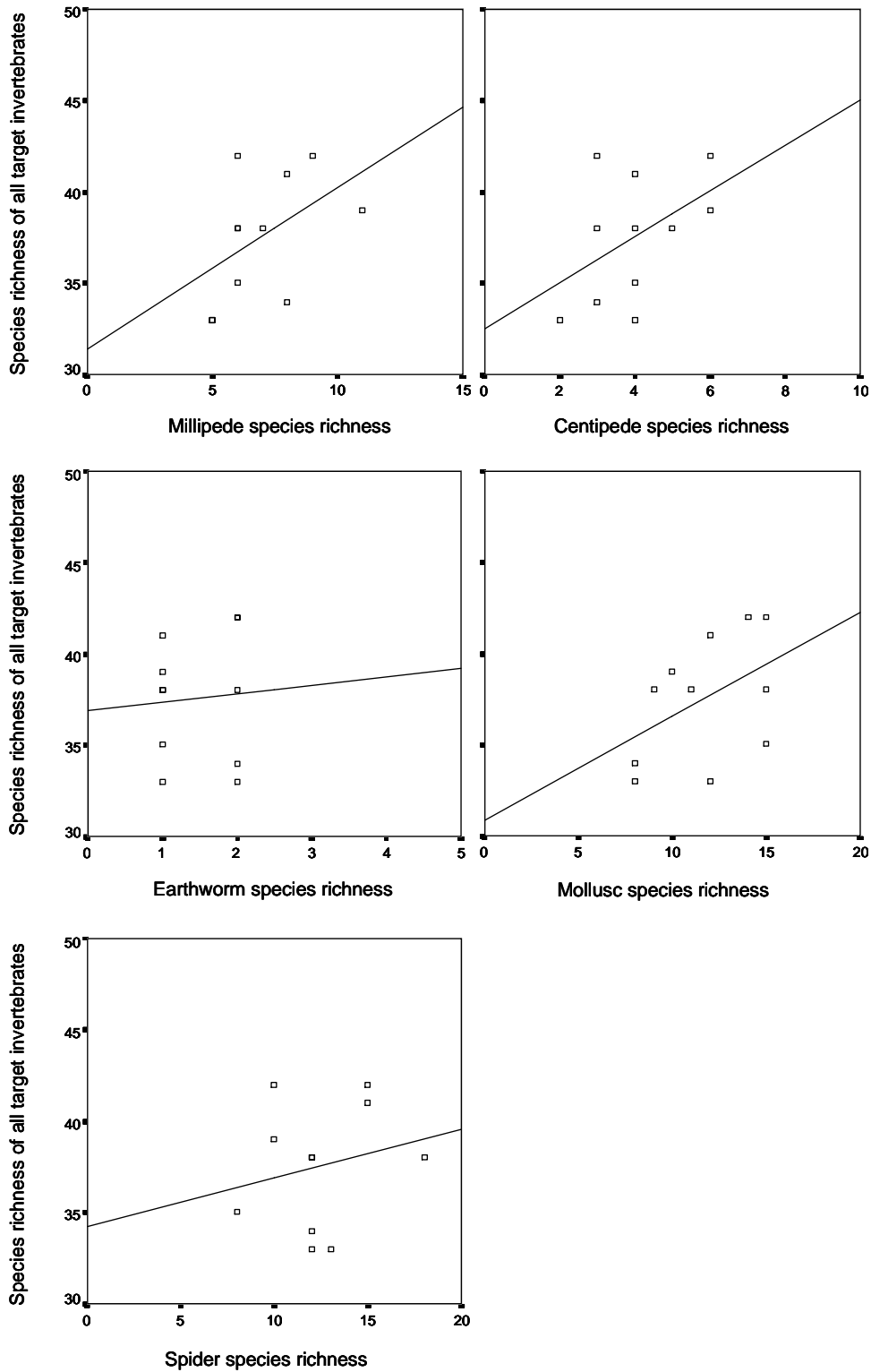


Figure 5.1: The use of individual invertebrate taxa as indicators of the species richness of all indigenous target invertebrates. Note that none of these relationships were significant.

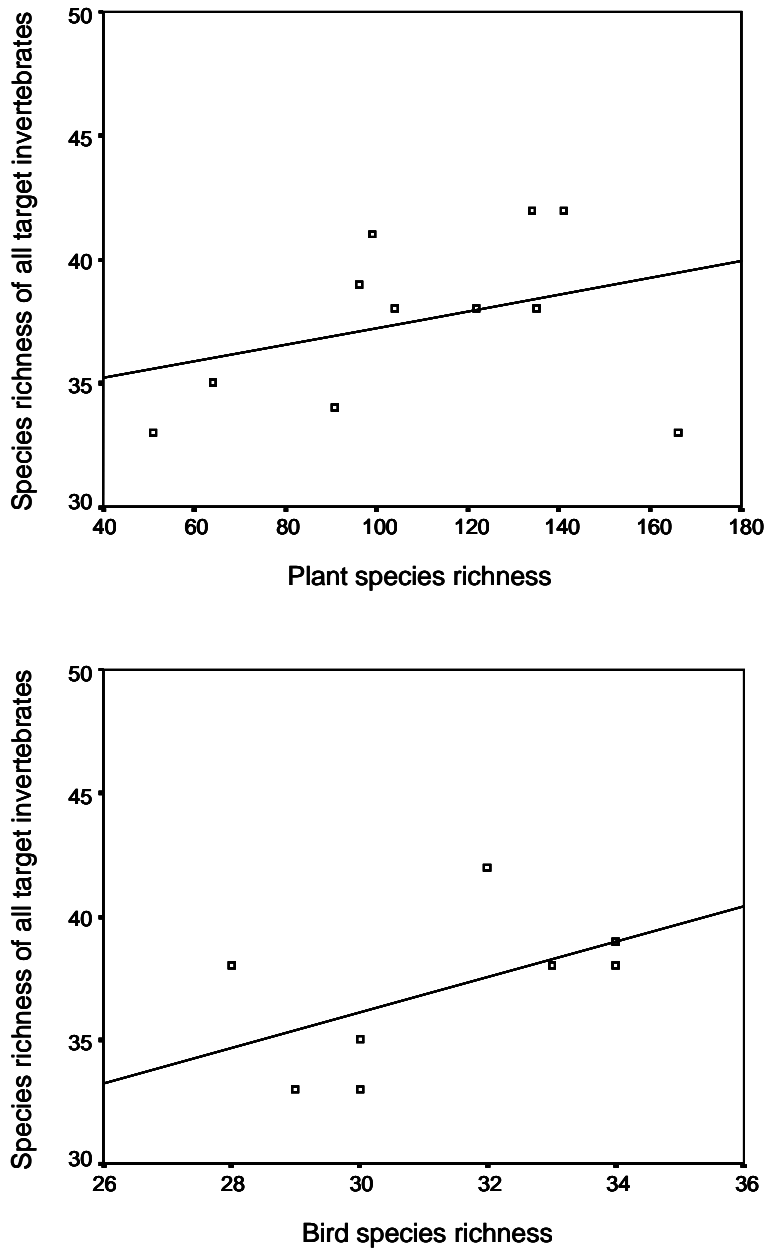


Figure 5.2: The use of individual non-invertebrate taxa as indicators of the species richness of all indigenous target invertebrates. Note that neither relationship was significant.

Table 5.3: Relationship matrix for species richness (S) of invertebrates, plants and birds in Limpopo Province forests (R = linear regression results, C = Pearson's correlation coefficient). The only significant relationship was between millipede and centipede richness.

Group	Millipede S	Centipede S	Earthworm S	Mollusc S	Spider S	Plant S
Centipede S	R $R^2 = 0.531^*$ R $F_{1,10} = 10.200^*$ C 0.729*	- - -				
Earthworm S	R $R^2 = 0.000$ R $F_{1,10} = 0.000$ C 0.000	R ² = 0.023 $F_{1,10} = 0.211$ 0.151	- - -			
Mollusc S	R $R^2 = 0.014$ R $F_{1,10} = 0.127$ C -0.118	R ² = 0.007 $F_{1,10} = 0.067$ -0.086	R ² = 0.033 $F_{1,10} = 0.311$ -0.183	- - -		
Spider S	R $R^2 = 0.098$ R $F_{1,10} = 0.979$ C -0.313	R ² = 0.099 $F_{1,10} = 0.984$ -0.314	R ² = 0.000 $F_{1,10} = 0.003$ -0.019	R ² = 0.096 $F_{1,10} = 0.951$ -0.309	- - -	
Plant S	R $R^2 = 0.003$ R $F_{1,10} = 0.029$ C -0.057	R ² = 0.073 $F_{1,10} = 0.707$ -0.27	R ² = 0.002 $F_{1,10} = 0.017$ -0.044	R ² = 0.199 $F_{1,10} = 2.237$ 0.446	R ² = 0.019 $F_{1,10} = 0.178$ 0.139	- - -
Bird S	R $R^2 = 0.410$ R $F_{1,10} = 4.174$ C 0.641	R ² = 0.430 $F_{1,10} = 4.536$ 0.656	R ² = 0.022 $F_{1,10} = 0.136$ 0.149	R ² = 0.116 $F_{1,10} = 0.790$ -0.341	R ² = 0.042 $F_{1,10} = 0.261$ 0.204	R ² = 0.005 $F_{1,10} = 0.032$ 0.073

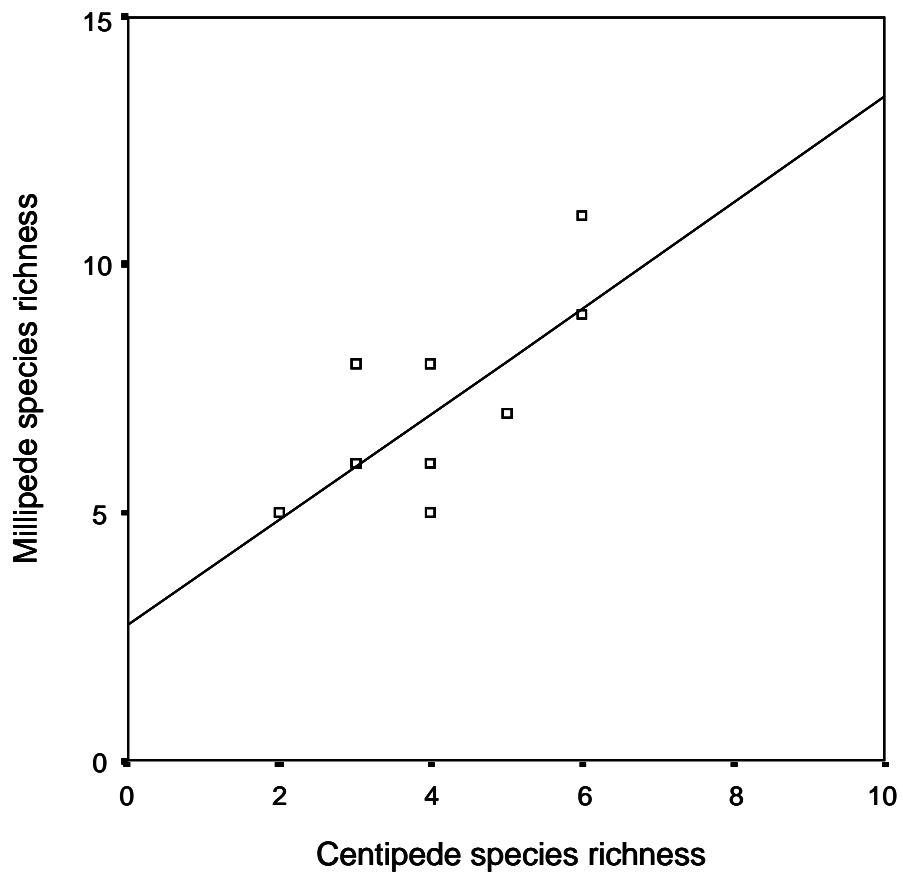


Figure 5.3: The use of centipedes as indicators of millipede species richness. The relationship between centipede and millipede species richness was significant.

5.3.2 Higher taxa as indicators of invertebrate species richness

The target group species sampled were not distributed evenly across genera and families and the numbers of representatives at each level varied according to target group (Figures 5.4, 5.5 and 5.6).

There was a significant positive relationship between the invertebrate species richness of target groups and genera richness in Limpopo Province forests (Table 5.4, Figure 5.7). The positive relationship between species richness and family richness was also significant (Table 5.4, Figure 5.7). These results suggest that both the genus and family levels could be used as reliable surrogates for invertebrate species richness. It is interesting to note that the genera: family relationship was positive, but not significant.

Table 5.4: Relationship matrix for species, genus and family richness (*S*) of target group invertebrates in Limpopo Province forests (R = linear regression results, C = Pearson's correlation coefficient).

		Species <i>S</i>	Genus <i>S</i>
Genus <i>S</i>	R	$R^2 = 0.576, F_{1,10} = 12.227^{**}$	-
	C	0.759 ^{**}	-
Family <i>S</i>	R	$R^2 = 0.435, F_{1,10} = 6.928^*$	$R^2 = 0.239, F_{1,10} = 2.819$
	C	0.660 [*]	0.488

Probability: * $P < 0.05$; ** $P < 0.01$

Although they were both significant, the genus:species relationship was stronger than the family:species relationship based on R^2 values and Pearson's correlation coefficients. The genus:species regression also more closely approximated the 45° slope than the family:species regression (Figure 5.7).

All forests were ranked in order of decreasing target group richness (*S*) at each taxonomic level (Table 5.5). The ranking order of forests at each level was different, illustrating that the taxonomic level used in invertebrate surveys in Limpopo Province forests has important effects on richness calculations and conservation prioritization.

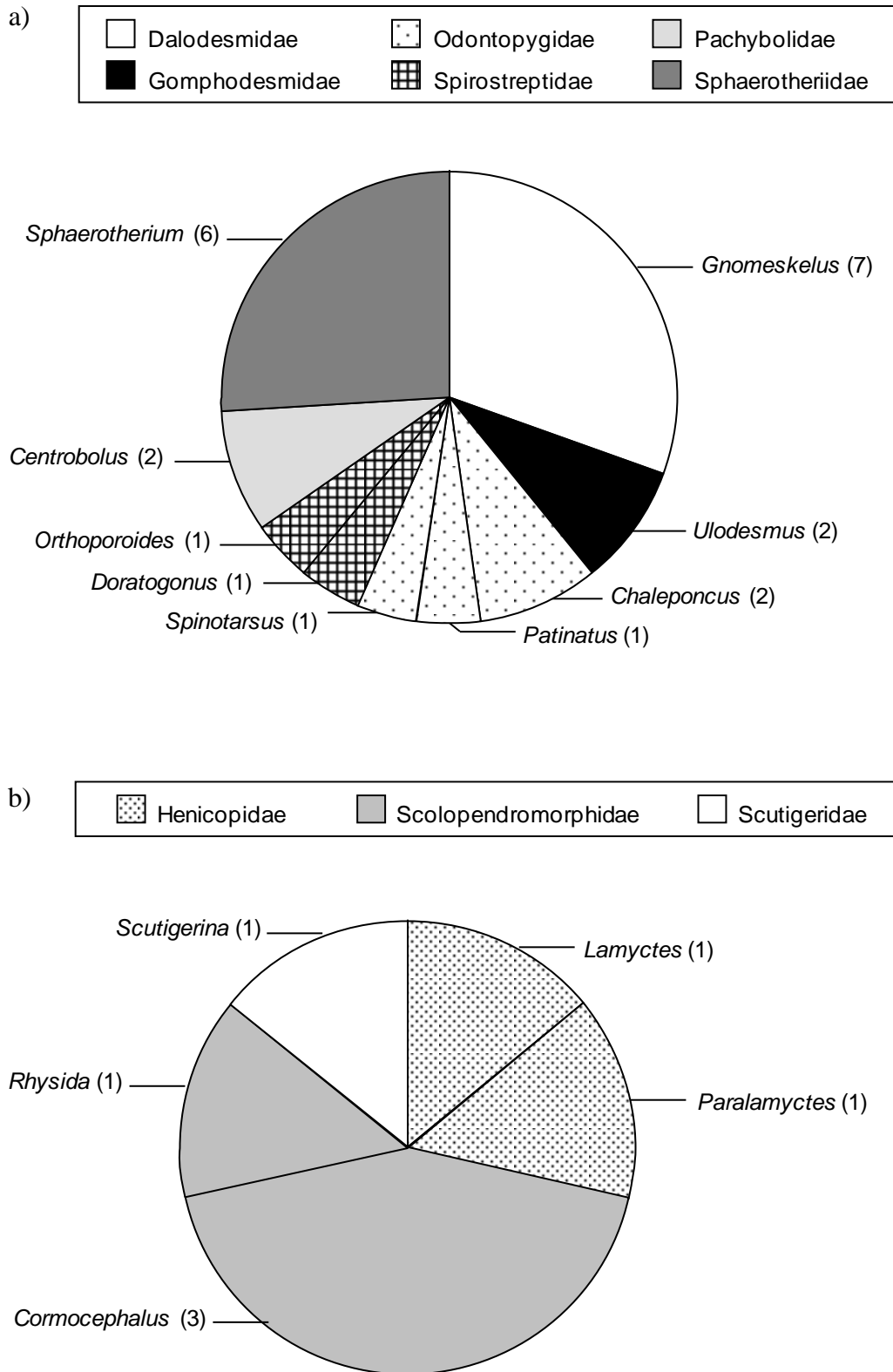


Figure 5.4: Distribution of indigenous species among families and genera in all Limpopo Province forests for a) millipedes and b) centipedes. The number of species in each genus is indicated in parentheses. The Geophilomorpha have been excluded from the centipede graph since they could not be identified beyond order level.

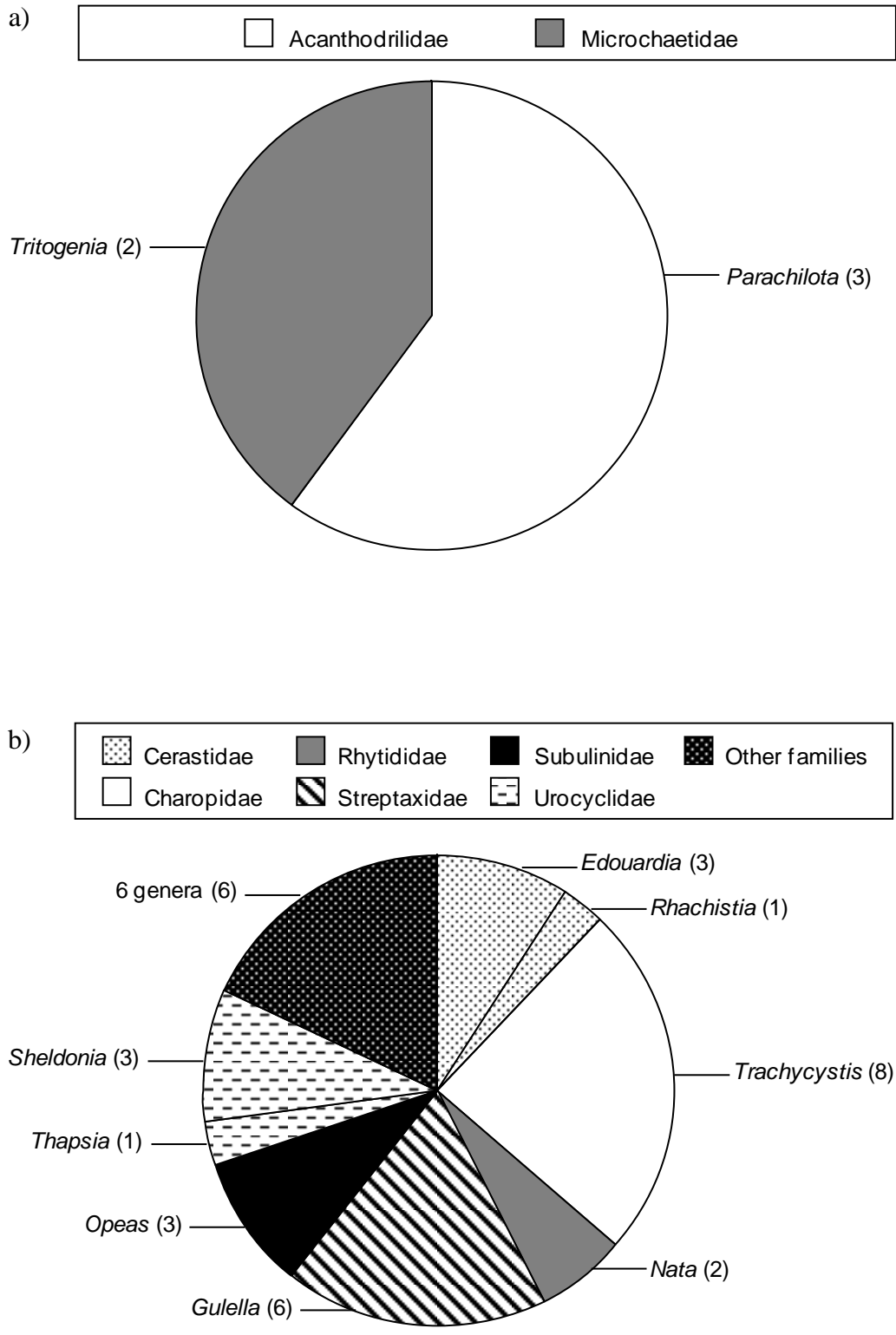


Figure 5.5: Distribution of indigenous species among families and genera in all Limpopo Province forests for a) earthworms and b) molluscs. The number of species in each genus is indicated in parentheses. ‘Other families’ of molluscs include Achatinidae, Chlamydephoridae, Clausiliidae, Euconulidae, Helicarionidae and Pomatisidae, each with one genus and one species.

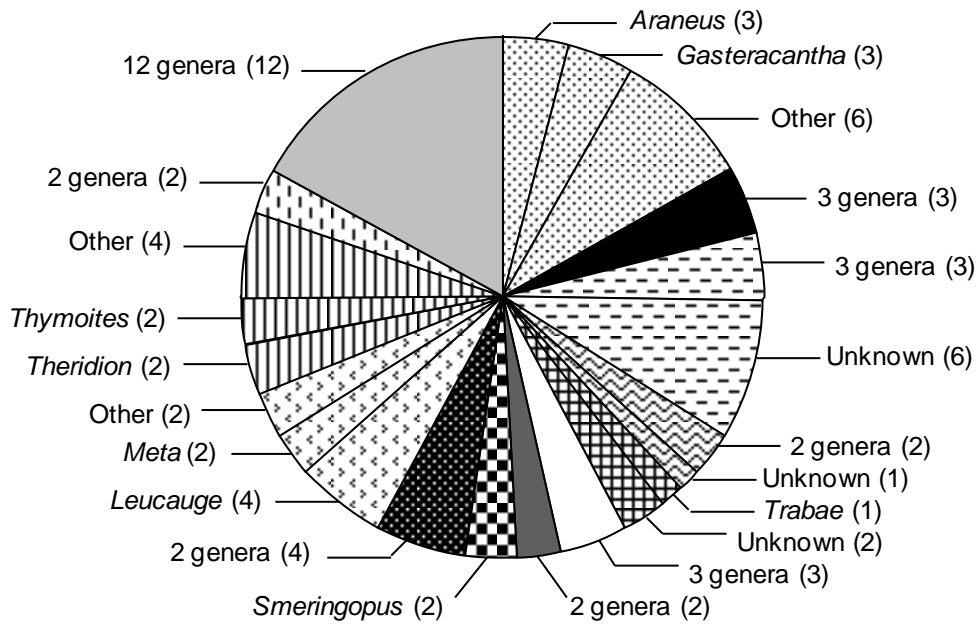
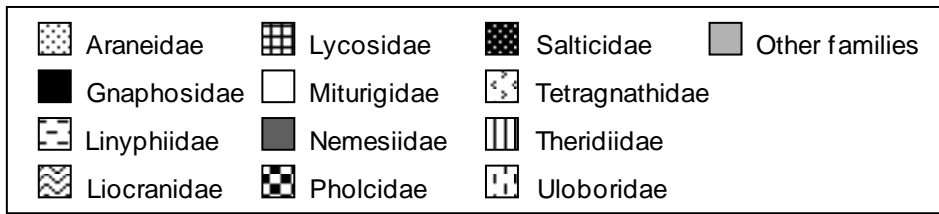


Figure 5.6: Distribution of indigenous spider species among families and genera in all Limpopo Province forests. The number of species in each genus is indicated in parentheses. Only genera with two or more species are named. ‘Other families’ of spiders include Anapidae, Clubionidae, Corinnidae, Ctenidae, Cyatholipidae, Dipluridae, Hahniidae, Mimetidae, Nesticidae, Orsolobidae, Phyxelididae and Zodariidae, each with one genus and one species.

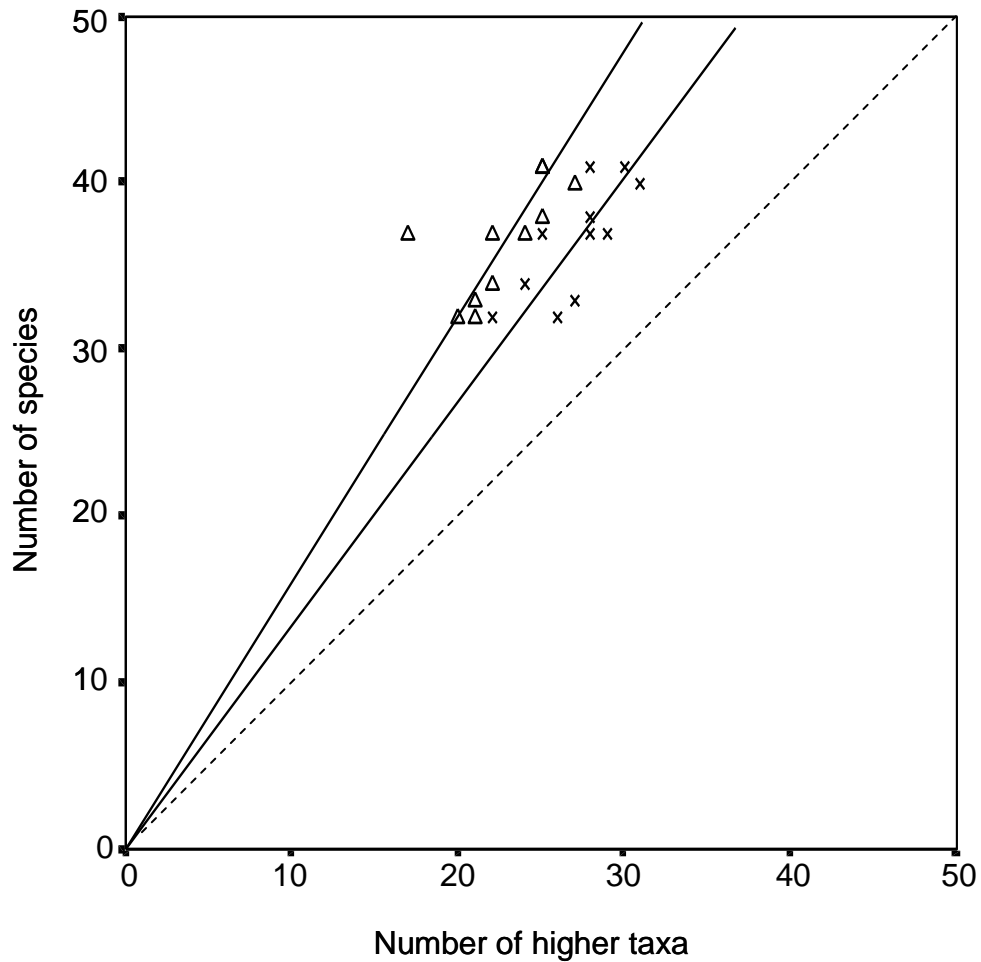


Figure 5.7: The use of higher taxa as surrogates of species richness, comparing the genus (x) and family (Δ) levels to species. The values represent the 11 forests sampled. The genera are better surrogates because they more closely approximate the 45° angle (dotted line).

Table 5.5: Ranking of forests for hypothetical conservation prioritization, in order of decreasing richness at three taxonomic levels. Parentheses indicate the richness (S) of forests at each taxonomic level.

<i>Rank</i>	<i>By species</i>	<i>By genera</i>	<i>By families</i>
1	Entabeni (41)	Roodwal (31)	Roodewal (27)
2	New Agatha (41)	Entabeni (30)	Entabeni (25)
3	Roodewal (40)	Ratombo (29)	New Agatha (25)
4	Baccarat (38)	Hanglip (28)	Baccarat (25)
5	Hanglip (37)	New Agatha (28)	Hanglip (24)
6	Ratombo (37)	Baccarat (28)	Grootbosch (22)
7	Grootbosch (37)	Goedehoop (27)	Forest Glens (22)
8	Forest Glens (34)	Thathe Vondo (26)	Goedehoop (21)
9	Goedehoop (33)	Grootbosch (25)	Thathe Vondo (21)
10	Thathe Vondo (32)	Forest Glens (24)	Swartbos (20)
11	Swartbos (32)	Swartbos (22)	Ratombo (17)

5.3.3 Morphospecies as indicators of formal (true) invertebrate species richness

The total number of morphospecies identified in each forest was compared to the total number of true species as determined by specialists. In all cases the assumptions of the ANOVA were met (Kolmogorov-Smirnov test $P > 0.05$). The results showed that the morphospecies approach significantly overestimated total species richness ($F_{1,21} = 14.250$, $P = 0.001$, Figure 5.8). However, there was a significant correlation between total morphospecies richness and true species richness (Linear regression: $R^2 = 0.394$, $F_{1,10} = 5.863$; Pearson's correlation coefficient: 0.628 , $P = 0.039$).

The differences between morphospecies and true species numbers varied according to group (Figure 5.9). Millipede ($F_{1,21} = 8.150$, $P = 0.010$), earthworm ($F_{1,21} = 7.775$, $P = 0.011$) and mollusc ($F_{1,21} = 6.915$, $P = 0.016$) morphospecies significantly overestimated the true species richness of that group. In contrast, there were no significant differences between the morphospecies and true species richness in centipedes ($F_{1,21} = 0.031$, $P = 0.861$), spiders ($F_{1,21} = 0.527$, $P = 0.476$) and ants ($F_{1,21} = 0.037$, $P = 0.849$). However, in all groups there was a significant correlation between the morphospecies and true species numbers (Figure 5.10, Table 5.6)

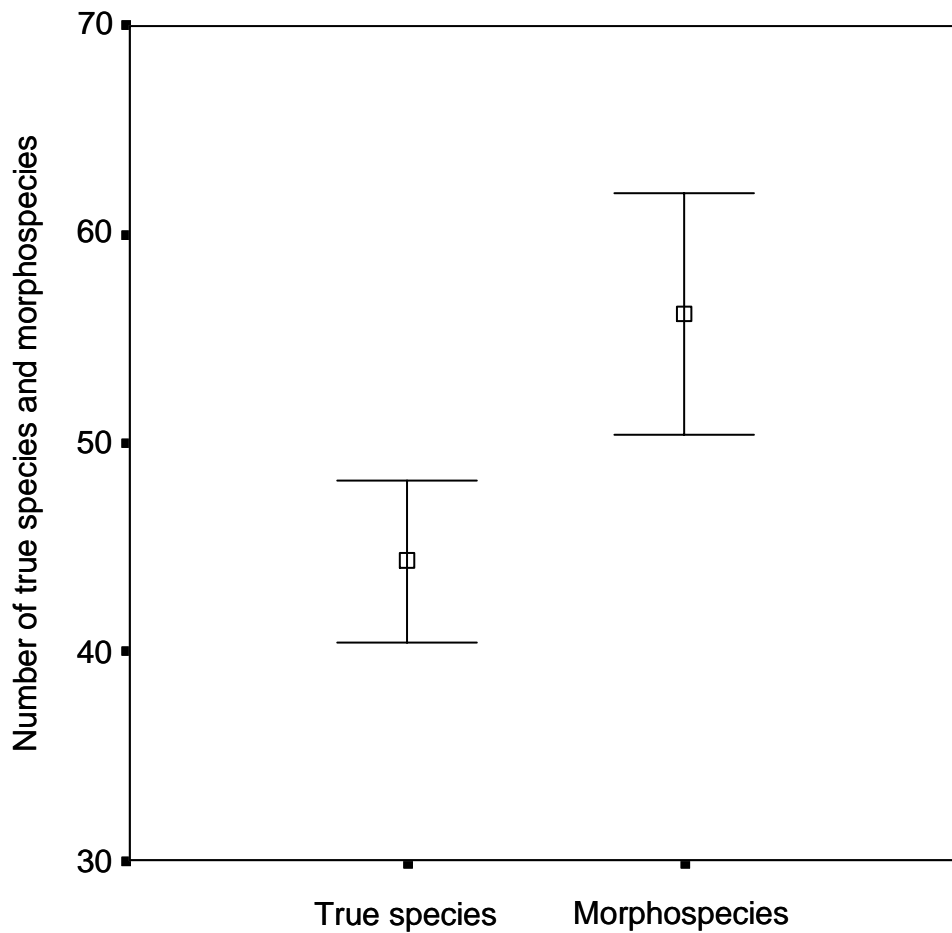


Figure 5.8: The total true invertebrate species richness (S) and morphospecies richness (S) of target groups and 95% confidence limits. The numbers include all indigenous and exotic target invertebrates and ants sampled by all methods, including randomly collected individuals.

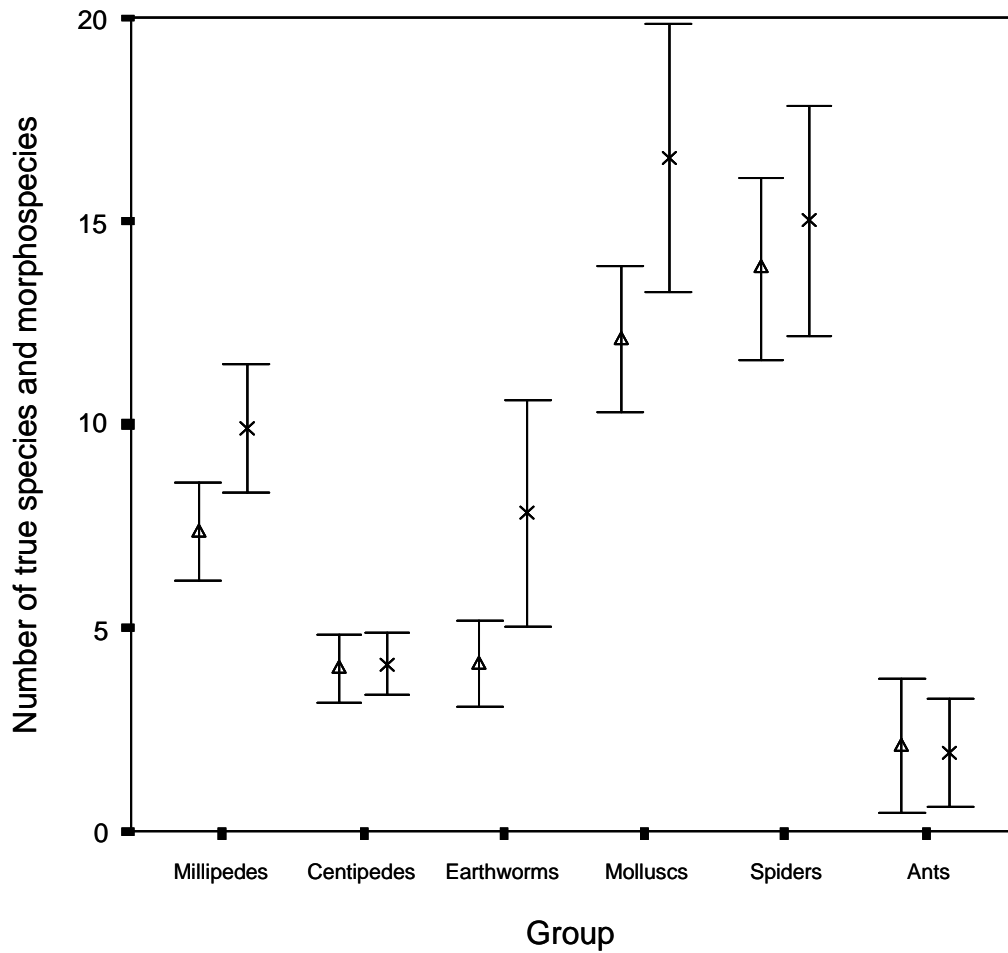


Figure 5.9: The true species richness (S , Δ) and morphospecies richness (S , x) of each invertebrate taxon and 95% confidence limits. The numbers include all indigenous and exotic invertebrates sampled with all methods, including randomly collected individuals.

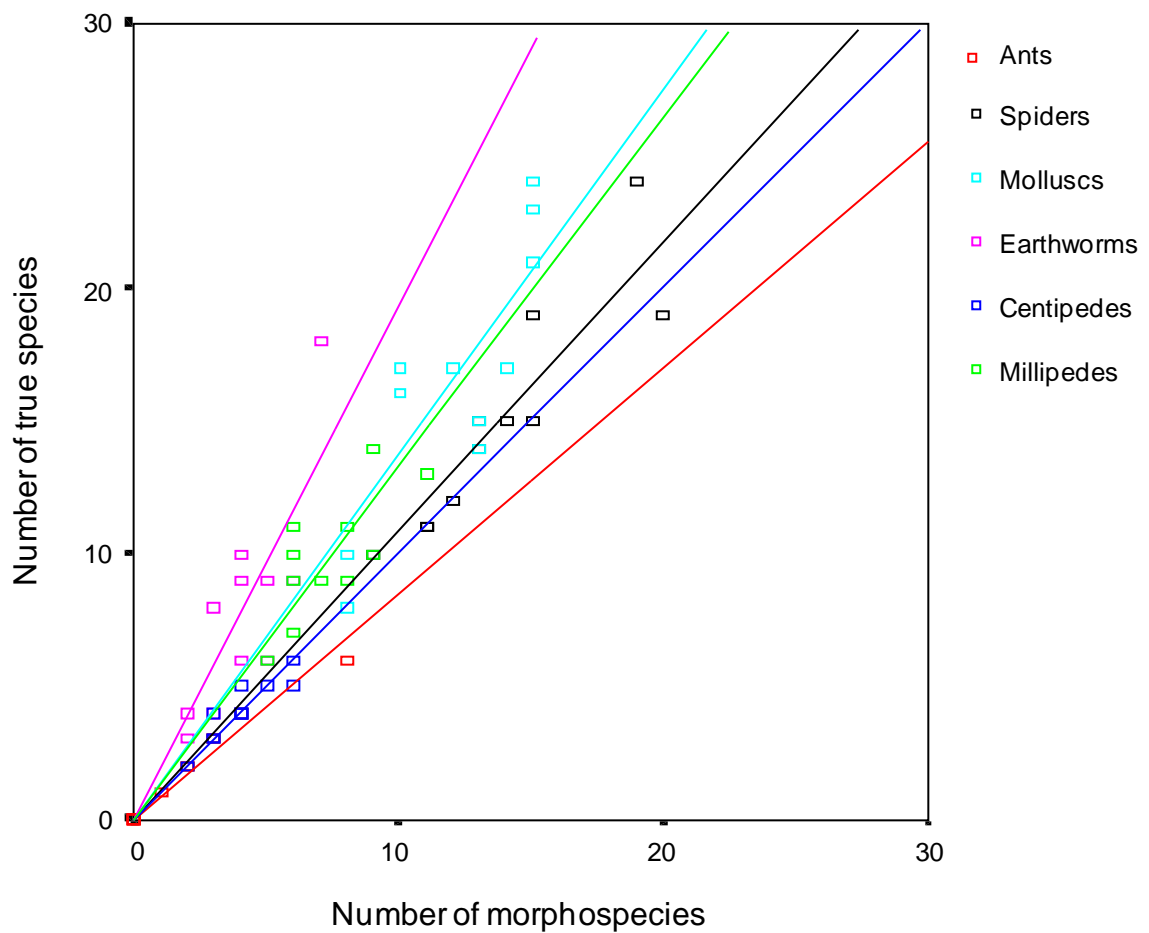


Figure 5.10: The use of morphospecies as surrogates of species richness for each invertebrate group. Centipede morphospecies most accurately reflects true species because this line most closely approximates the 45° angle. Earthworm morphospecies numbers were the least accurate.

Table 5.6: Summary of the relationships between the morphospecies richness (S) and true species richness (S) of each group investigated. Note that all relationships were significant ($P < 0.01$)

	Linear Regression R^2	Linear Regression $F_{1,10}$	Pearson's coefficient	P
Millipedes	0.550	11.02	0.742	0.009
Centipedes	0.818	40.511	0.905	< 0.001
Earthworms	0.662	17.591	0.813	0.002
Molluscs	0.715	22.533	0.845	0.001
Spiders	0.828	43.367	0.910	< 0.001
Ants	0.967	267.729	0.984	< 0.001

Although they were all significant, the strength of the correlation between morphospecies and true species varied by group. Based on R^2 and correlation coefficient values, the strongest relationship was found in the ant group and the weakest relationship in the millipedes (Table 5.6). Sorting accuracy also varied according to group. Centipede morphospecies most closely matched true species, since this regression most closely approximated the 45° slope (Figure 5.10). Morphospecies for the earthworm group were the poorest match to true species. These results show that certain groups were more accurately sorted than others were.

In all cases, the differences between morphospecies and true species numbers were the direct result of splitting or lumping true species. The degree of correct sorting and incorrect splitting and lumping of true species in total and in each group are given in Figure 5.11. These results highlight the percentage and cause of the mistakes made in sorting each taxon.

The three groups with the highest percentage of mistakes were earthworms, molluscs and millipedes. Sorting faults were made in all earthworm genera, but *Amyntas* and *Parachilota* species respectively accounted for 31% and 22% of all mistakes. Mollusc mistakes were most often made with the *Trachycystis* (29%), *Gulella* (21%) and *Nata* (21%) species. Most (67%) millipede sorting mistakes occurred with *Sphaerotherium* species and a single species, *S. cf. mahaium* Schubart, 1958, accounted for 60% of all *Sphaerotherium* sorting faults.

In general, these results show that morphospecies can be used as an accurate surrogate for invertebrate species in Limpopo Province forests, but overestimation of diversity is likely to occur. The accuracy of morphospecies varied considerably according to the taxa considered, so groups surveyed in this way must be chosen with care.

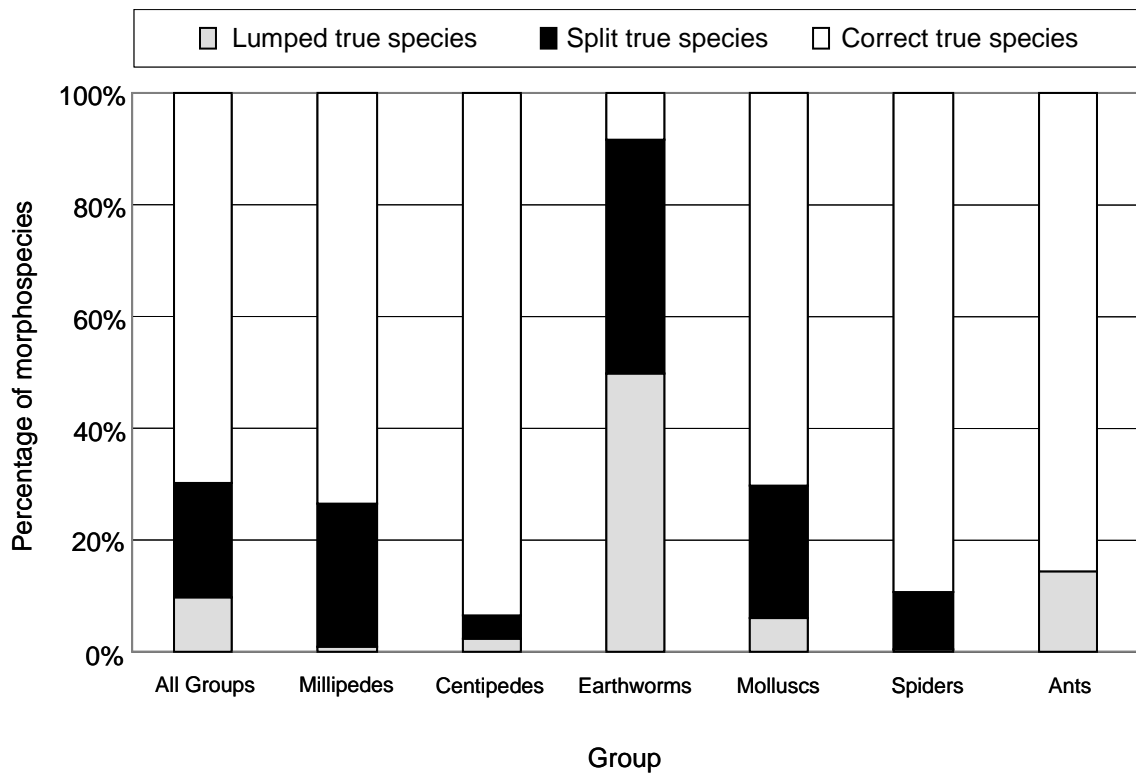


Figure 5.11: The relative amount of splitting and lumping of true species when using morphospecies. ‘All groups’ includes the taxa shown, amphipods and scorpions.

5.3.4 Vegetation classification as a surrogate for invertebrate species' distributions

Invertebrate species' distributions were largely correlated with forest subtype. Table 4.1a (pg. 105) and Figure 4.4a (pg. 110) show that the strongest similarities in invertebrate species composition were found in forests of the same subtype. However, Figure 4.1a (pg. 106) illustrates that each forest subtype contains species unique to that habitat.

These results suggest that forest classification does provide some insight into invertebrate species distribution patterns in Limpopo Province forests.

5.4 DISCUSSION

5.4.1 Individual taxa as indicators of species richness

Many individual taxa have been suggested as indicators of wholesale invertebrate biodiversity. Plants, in particular, are commonly used as surrogates for total biodiversity and as the primary criterion for the identification of biodiversity hotspots (Myers 1988; 1990; Mittermeier *et al.* 1998). The diversity of plants has been shown to promote the diversity of insects (Knops *et al.* 1999) and studies have found statistically significant correlations between plant and invertebrate richness in various habitats (Lycaenidae:vascular plant relationship in Erhardt & Thomas 1991; Moritz *et al.* 2001; Negi & Gadgil 2002; Schwab *et al.* 2002). However, not all studies have found such correlations (Oliver *et al.* 1998; Vessby *et al.* 2002). The richness of various vertebrate groups has also been shown to correlate with the richness of selected invertebrate taxa (Oliver *et al.* 1998; Moritz *et al.* 2001; Vessby *et al.* 2002)

To test if a single taxon could indicate the total richness of target invertebrate groups in Limpopo Province forests, all sufficiently rich invertebrate groups sampled in this study, as well as plants and birds, were examined as potential indicators. However, no significant relationships were found between total target group forest invertebrate richness and millipede, centipede, earthworm, mollusc, spider, plant or bird richness (Table 5.2, Figures 5.1 and 5.2). This suggests that all of these taxa would perform poorly as indicators of target invertebrate richness and therefore, total invertebrate species richness. These results

were similar to those of Lawton *et al.* (1998) who assessed butterflies, flying beetles, canopy beetles, canopy ants, leaf-litter ants, termites, soil nematodes and birds as diversity indicators in a tropical Cameroon forest and found that no single group was a good indicator of total richness. Many other authors have questioned the use of indicator species to predict wholesale species richness (Majer 1983; Prendergast *et al.* 1993; Ehrlich 1994; Lombard 1995; Oliver & Beattie 1996a; Kerr 1997; Prendergast & Eversham 1997). In fact, even if a single taxon had been found in the current study to correlate significantly with total target invertebrate richness in Limpopo Province forests, it could only be suggested as a good indicator of the groups examined. Its value as an indicator of total invertebrate biodiversity would remain untested.

Although it was not significant, the relatively strong relationship between bird richness and total target invertebrate richness was surprising. The richness of any single invertebrate taxon was expected to correlate more closely to the total target invertebrate richness than the more distantly related birds. The reason for this pattern is not evident.

With the exception of millipedes and centipedes, none of the individual taxa investigated in the present study could reliably indicate the richness of any other group (Table 5.3). Several recent studies that included similar analyses have also found few correlations in richness across taxa, although results have been mixed and have yielded few generalizations (Table 5.7). Howard *et al.* (1998) showed that there was low congruence between the species richness of moths, butterflies, birds and small mammals in Ugandan forests. Prendergast *et al.* (1993) found little coincidence of richness hotspots for birds, butterflies, dragonflies, liverworts and aquatic angiosperms in Britain. According to Gaston (1996) most known relationships between the species richness of different taxa are positive, but statistically strong correlations are rare.

Table 5.7: Summary of significant correlations in taxon richness across sites in various habitats (Significant correlations: $P < 0.05$), listed in order of decreasing proportion of significant positive correlations. Only recent (1996+) studies that have included invertebrate taxa are listed.

Habitat	Place	Taxa investigated	Proportion of significant correlations	Proportion of significant positive correlations	Reference
Rainforests	Queensland, Australia	Plants, insects, snails, vertebrates	6/6 (100%)	6/6 (100%)	Moritz <i>et al.</i> 2001
Hay meadows	North-eastern Switzerland	Angiosperms, spiders, true bugs	3/3 (100%)	3/3 (100%)	Schwab <i>et al.</i> 2002
Forests	Uganda	Woody plants, large moths, butterflies, birds, small mammals	3/10 (30%)	3/10 (30%)	Howard <i>et al.</i> 1998
Temperate forests	Indian Garhwal Himalaya	Macrolichens, mosses, liverworts, woody plants, ants	7/10 (70%)	3/10 (30%)	Negi & Gadgil 2002
Afromontane forest	KwaZulu-Natal, South Africa	Spiders, ground beetles, rove beetles, ants	1/6 (16%)	1/6 (16%)	Kotze & Samways 1999b
Semi-natural grasslands	South-central Sweden	Plants, ground beetles, dung beetles, butterflies, bumblebees, birds	7/45 (15%)	6/45 (13%)	Vessby <i>et al.</i> 2002
Natural and plantation forests	South-central Cameroon	Butterflies, flying beetles, canopy beetles, canopy ants, leaf-litter ants, termites, soil nematodes, birds	4/36 (11%)	3/36 (8%)	Lawton <i>et al.</i> 1998
Multiple-use forest	Eastern Australia	Plants, ants, beetles, mammals, birds, frogs, reptiles	8/42 (19%)	3/42 (7%)	Oliver <i>et al.</i> 1998
Indigenous forests	Limpopo Province, South Africa	Plants, millipedes, centipedes, earthworms, terrestrial molluscs, spiders, birds	1/21 (5%)	1/21 (5%)	This study
Forests	New South Wales, Australia	Ants, beetles, spiders	1/3 (33%)	0/3 (0%)	Oliver & Beattie 1996a
Meadows, aspen forests, conifer forests	Colorado, USA	Butterflies and moths	0/1 (0%)	0/1 (0%)	Ricketts <i>et al.</i> 2002

According to Landres *et al.* (1988), the implicit assumption in the use of indicators is that they provide an assessment of habitat quality and that if the habitat is favourable for the indicator, conditions will be suitable for other species. Therefore, positive correlation is most likely to occur among closely related taxa or groups in the same guild, which includes taxa that use and respond to habitat in similar ways, exploit the same class of resources and have similar breeding characteristics, foraging behaviours, diet and habitat requirements. The unique significant positive correlation between millipede and centipede richness in the present study (Figure 5.3) was somewhat anticipated, since they are the most similar of the target taxa investigated in terms of mobility and body size range. Although they have different functional roles, millipedes and centipedes have similar microhabitat requirements and could be expected to respond to environmental conditions in similar ways. The single significant positive correlation in species richness found by Kotze and Samways (1999b) was between closely related invertebrate groups with similar requirements: ground beetles (Carabidae) and rove beetles (Staphylinidae). However, Ricketts *et al.* (2002) found no correlation between moth and butterfly diversity in Colorado, USA, although these two groups are relatively closely related. In some cases, behavioural traits, such as nocturnality, can overwhelm phylogeny and other ecological similarities in determining correlations in diversity (Ricketts *et al.* 2002). Clearly, phylogenetic relatedness, although intuitive, is not a reliable criterion for selecting appropriate indicator taxa (Holl 1996; Ricketts *et al.* 2002).

The significant correlation between millipede and centipede richness in Limpopo Province forests does have a possible practical application. There were fewer centipede species (7) and individuals (3247) than millipede species (24) and individuals (3372) sampled in the study area, so sorting and identification of centipedes would be more efficient than millipedes. Therefore, centipedes alone could be sampled and identified and the ratio of centipedes to millipedes determined in the present study could be used to predict millipede richness in these forests with some degree of accuracy. This would effectively reduce the costs and time associated with surveying both myriapod groups. However, this application is of limited use in conservation since it only provides insight into a small proportion of the total invertebrate diversity of Limpopo Province forests and may be applicable only on a regional or habitat scale.

Overall, these results support the assertion made by Lawton *et al.* (1998) that attempts to assess the richness of many taxa using one or a limited number of indicator taxa may be highly misleading. Because neither conceptual nor empirical considerations support the use of indicator species as surrogates for other species, this approach should be avoided (Landres *et al.* 1988). The results presented in this chapter suggest that without confirmatory research, it is inappropriate to use any single taxon as an indicator of total invertebrate biodiversity in Limpopo Province forests. Given these results, all of the information presented in the current study should be examined with caution, since only a limited number of target groups were sampled during this study and they cannot be assumed to represent all invertebrate diversity in Limpopo Province forests. Additional invertebrate taxa with higher mobility (i.e. flying insects) and different life histories (i.e. complete metamorphosis, social insects), functional roles (i.e. pollinators) and body sizes should also be investigated in Limpopo Province forests before any generalizations regarding all invertebrates can be accurately made.

5.4.2 Higher taxa as indicators of invertebrate species richness

There was a significant positive relationship between total target invertebrate species richness and genera and family richness in Limpopo Province forests (Table 5.4), suggesting that the higher taxon approach could be used as a reliable biodiversity surrogate. The results of the current study were similar to those of Balmford *et al.* (1996), who found that genera, family and order richness of birds, mammals and angiosperms were significantly related to the total species richness of each group. Interestingly, the relationship was the least robust for speciose higher taxa. Pik *et al.* (1999) and Andersen (1995) both showed strong correlations between genus and species richness in Australian ant communities. Additional studies (Roy *et al.* 1996) have also successfully demonstrated that higher taxa can be used in biodiversity surveys. Despite the apparent success of these studies, others have shown poor correlations between species richness and various higher taxonomic levels (McAllister *et al.* 1994; Prance 1994; Andersen 1995).

In the present study, the genus level was a more accurate surrogate for species richness than families (Figure 5.7), but this is not surprising. One would expect progressively higher taxonomic levels to be more and more weakly linked to species richness (Gaston & Williams 1993; Balmford *et al.* 1996).

However, the use of any higher taxonomic level in invertebrate studies is questionable. Higher taxa that comprise many species are poorer indicators of species richness than those containing fewer species (Gaston & Blackburn 1995; Balmford *et al.* 1996). Further, the predictive power of higher taxon surrogates is generally lowest for the richest sites (Balmford *et al.* 1996). These limitations are important for invertebrates because many invertebrate groups are speciose and many habitats support rich invertebrate communities. Therefore, higher taxon surrogacy is the least reliable for the organisms it would benefit most (Anderson 1995). According to Balmford *et al.* (1996), this is the ‘cruel bind’ of higher taxa surrogates, since the more species a given higher taxon represents in a rich site, the more time and effort are saved.

Some of the problems associated with higher taxa surrogates can be illustrated by the present study, where species were not distributed evenly across genera and families and some taxa were more speciose than others (Figures 5.4, 5.5 and 5.6). On the family level, molluscs were twice as rich as millipedes. However, molluscs were only 56% richer than millipedes in genera and only 43% richer in species. The reverse trend is evident between molluscs and spiders. Spiders were twice as rich as molluscs on the family level, but were more than 115% richer in species. Such discrepancies could mislead conservation efforts, as demonstrated by the ranking of Limpopo Province forests according to richness at each taxonomic level (Table 5.5). The forests that appear in the top five for each level are surprisingly consistent, but there are important exceptions to this trend. Ratombo, for example, was ranked in position six based on species richness, position three based on genus richness and position 11 (last) based on family richness.

There are also difficulties associated with using the higher taxon approach when attempting to incorporate endemics into conservation planning. According to Prance (1994), important sites for conservation are centres of endemism, species diversity and habitat diversity. At higher taxonomic levels, few of these centres are evident and centres of endemism may not coincide with centres of species (or higher level) diversity. Therefore, genus or family level data cannot be used to promote efficient species level conservation (van Jaarsveld *et al.* 1998) and the species level should be the focus when assessing biodiversity for conservation planning.

Although target group invertebrate species richness corresponded significantly with genera and families in Limpopo Province forests, the higher taxon approach must be used with caution because (1) the inequality in species distributions across higher taxa undermines the accuracy of higher taxa as indicators; (2) trends found on the species level may not be reflected at higher levels and different forests may be prioritised for conservation depending upon the taxonomic level investigated and (3) important site assets, such as endemism, species diversity and habitat diversity may be overlooked when using taxonomic levels other than species. Therefore, the higher taxon approach cannot be recommended for use in Limpopo Province forests, particularly for invertebrate studies.

5.4.3 Morphospecies as indicators of invertebrate species richness

Comparisons between morphospecies and true species show that morphospecies significantly overestimated the total target invertebrate species richness in Limpopo Province forests (Figure 5.8). The relationship between total morphospecies and total true species was significant, but richness estimations would have been inaccurate if morphospecies alone were used. This is in contrast to Oliver and Beattie (1996a) and Oliver and Beattie (1993) who showed consistent results regardless of whether true species or morphospecies were used.

Although the relationships between true species and morphospecies were significantly positive for all taxa included in the present study (Table 5.6), certain invertebrate groups were more prone to sorting errors. Splitting mistakes were generally made more often than lumping and this resulted in the significant overestimation of richness in three groups: earthworms, millipedes and molluscs (Figure 5.9). Because individuals in these groups were relatively large, all sorting was done by eye without the aid of a microscope. Earthworms were sorted with the least success, followed by molluscs and millipedes (Figures 5.10 and 5.11). In the case of earthworms, inaccuracies were largely due to the fact that individuals are identified to true species largely on the basis of internal characteristics and can appear alike externally. There was also a high degree of size variation between juveniles and adult earthworms of the same species. Oliver & Beattie (1993) had similar results when sorting spiders, ants, marine polychaetes and mosses; they found that the highest proportion of sorting mistakes was made with polychaetes. Although the characters used in species identification of polychaetes are different from

earthworms (Branch & Branch 1981; Davies 1991), they are both segmented worms belonging to the phylum Annelida. However, the results of the current study contradict Paoletti (1999) who states that ‘earthworm taxonomy is reasonable straightforward even for non-experts.’ Millipede mistakes were mostly made because of colour and size variation within a single species and this was particularly marked in *Sphaerotherium* individuals. Mollusc mistakes were usually made when juveniles appeared to be somewhat different from adults and morphospecies were split because of uncertainty.

Sorting accuracy may have also been related to volume, since earthworms, millipedes and molluscs represent three of the four most frequently sampled groups and accounted for about 66% of all individuals sampled during this study (Table 5.8). Generally, as the number of individuals to be sorted increased, so did the degree of overestimation. Only centipedes were an important exception to this trend. Accuracy did not appear to be related to taxon richness (Table 5.8). These results were contrary to Oliver and Beattie (1996a) who found that misidentification of true species was more common in rich families.

Table 5.8: Sampling frequency, richness and morphospecies error for invertebrate groups. ‘Other’ taxa are those that were not considered for the morphospecies analysis and include amphipods, scorpions, butterflies, dragonflies, flies and non-target invertebrates sampled in pitfall traps.

<i>Taxon</i>	<i>Number of individuals</i>	<i>Percentage of total</i>	<i>True species richness (S)</i>	<i>Error (% mistakes)</i>
Earthworms	8145	39.49	17	91.86
Millipedes	3372	16.35	24	26.61
Centipedes	3247	15.74	7	6.67
Molluscs	2058	9.98	36	29.67
Spiders	696	3.37	70	10.91
Ants	113	0.55	12	14.29
Other	2996	14.52		
TOTAL	20627	100.00		

The groups sorted with the most success were centipedes, spiders and ants (Figures 5.10 and 5.11). Centipede species in Limpopo Province forests were distinct in size and colour and showed little individual variation within species. The same was generally true for

spiders and ants. However, the relative success with spider and ant morphospecies could have also been due to the fact that individuals were usually small and were sorted with the aid of a microscope. The accuracy of earthworm, millipede and mollusc sorting may have been increased if subjected to similar careful scrutiny.

The sorting accuracy of ants was not surprising, since studies have discussed the relative ease of accurate identification in this group (Oliver & Beattie 1993; 1996a). Pik *et al.* (1999) and Oliver & Beattie (1993) identified ants quite accurately using morphospecies. However, the low number of mistakes made when sorting spiders was not expected, since many spiders are sexually dimorphic and this can be a serious source of error for a non-specialist (Oliver & Beattie 1996a).

These results demonstrate that true species identification should be used in biodiversity surveys in order to obtain accurate richness estimates. However, if morphospecies must be used, training in species identification prior to sorting could certainly improve the accuracy of the morphospecies approach (Slotow & Hamer 2000). This is particularly important for groups that have high degrees of sexual dimorphism or polymorphism and for groups with many superficially similar taxa or many congeneric forms (New 1998). If using morphospecies, surveyors should also follow the example of Fabricus *et al.* (2003) and use specialized taxonomists to confirm the validity of RTUs. Further, reference collections and voucher specimens are essential to allow comparisons with other sites and for later verification or identification of specimens (Slotow & Hamer 2000).

5.4.4 Vegetation classification as a surrogate for invertebrate species' distributions

The apparent success of forest subtype as a surrogate for invertebrate species' distributions was unexpected, since several recent studies had only limited success with this method of surrogacy. York (1999) found that forest types used in New South Wales, Australia were poor surrogates for invertebrate species richness. However, in contrast to the present study, specific Australian forest types did not support characteristic invertebrate assemblages (York 1999). A study by Lombard *et al.* (2003) showed that land classes derived only from environmental and vegetation data can perform well as surrogates for plant distributions, but perform poorly for fauna. They advise that land classes should include species information from as many different taxa as possible, including plants,

vertebrates and invertebrates. York (1999) also advocates including invertebrates in forest classification systems.

The forest classification system followed here was derived from both environmental data and species data from many different taxonomic groups, but invertebrates were not considered (von Maltitz *et al.* 2003). It was therefore surprising that this system was at all successful as a surrogate for invertebrate species' distributions. Although invertebrates were ignored, the inclusion of many other taxonomic groups must have improved the prediction accuracy for many faunal groups and may be the reason for its apparent success as a surrogate for invertebrate distributions. This forest classification system suggested by von Maltitz *et al.* (2003) certainly can be seen as an improvement on some past classification systems.

When compared to past classification systems, the relative success of von Maltitz *et al.*'s (2003) classification system as a surrogate for invertebrate species' distributions becomes obvious. If the system proposed by von Maltitz *et al.* (2003) was used to set conservation priorities, we could assume that at least three forest patches would be reserved, including one of each subtype. According to the data presented here and in Chapter 4, many species unique to a single forest patch would be missed, but the majority of invertebrate species could be conserved. For example, if Grootbosch (mistbelt forest), Roodewal (semi-deciduous scrub forest) and Ratombo (semi-deciduous mixed forest) were conserved, approximately 63% of the invertebrate species sampled in the present study would be protected. In contrast, the system of Low and Rebelo (1996) only considers environmental and vegetation data, uses more broadly defined land classes and classifies all forests in Limpopo Province as a single type, Afromontane forest. Therefore, this land class would perform much more poorly as a surrogate for invertebrate species distributions and the majority of invertebrate species would be excluded from conservation.

According to Lombard *et al.* (2003), species that are unrepresented by broadly defined land classes tend to have small range sizes. Many of the invertebrates in Limpopo Province forests have restricted distributions (Chapter 4) so any land class surrogate used for invertebrates must be narrowly defined. Although the classification of von Maltitz *et al.* (2003) was relatively successful as a surrogate for invertebrate species distributions, its use

is not recommended here because of the site restricted species that could be overlooked in conservation prioritization.

5.5 CONCLUSION

According to the results of this chapter, patterns of invertebrate species richness in Limpopo Province forests cannot be accurately predicted using common surrogacy methods. No single taxon was found to be a reliable indicator of total target invertebrate richness in Limpopo Province forests; invertebrates cannot be excluded from biodiversity surveys based on the assumption that plants and vertebrates act as surrogates for invertebrate species richness (Oliver *et al.* 1998). Although the higher taxon method provided reliable approximations of target invertebrate species richness at the genus and family levels, species level trends may be masked and site assets such as endemism may be overlooked. The morphospecies approach shares these problems and it significantly overestimated total target invertebrate species richness and the richness in 50% of individual groups. Therefore, all of these widely used surrogacy methods were not supported.

Land classes (von Maltitz *et al.* 2003) were found to correlate with general target invertebrate species' distribution patterns. However, conservation prioritization may be misled if the habitat approach was used and many site restricted invertebrates could be excluded from conservation efforts. As a result, the predictive value of land classes for invertebrate species' distributions in Limpopo Province forests is questionable and this method is not recommended for conservation applications.

Overall, the results presented in this chapter suggest that there is no substitute for formal species in invertebrate studies where accurate richness estimations are desired and in conservation planning and prioritization. Because of the information associated with formally named species (i.e. endemism, threatened status, phylogenetic uniqueness), surrogate methods should be avoided whenever possible. If surrogates must be used, they should be applied with caution and with knowledge of their limitations. Because there is no 'best' surrogate, combinations of surrogates will be most practicable in most situations (Margules & Pressey 2000).

CHAPTER 6

SUMMARY AND CONSERVATION RECOMMENDATIONS

6.1 INTRODUCTION

This study investigated the biodiversity of selected Limpopo Province forest invertebrates and included analyses of species diversity, biogeography and surrogates. By focusing largely on aspects that have practical applications in conservation, this study provides much needed information to the Department of Water Affairs and Forestry (DWAF). The conservation of Limpopo Province forests is discussed in this chapter.

6.1.1 Uses of and threats to South African forests

South African forests play a role in the welfare of society that is disproportionately greater than their small size (Geldenhuys *et al.* 1986). Forest products are used directly by man for furniture and building timber, fuel wood, traditional medicines, food, materials for home crafts and decorative material (Geldenhuys & MacDevette 1989). Forests are also used for hunting, recreation and burial sites (Geldenhuys & MacDevette 1989; DWAF unpublished reports a & b). Indirect services are supplied by forests, such as protecting water catchments, preventing soil erosion and flooding, maintaining soil fertility, fixing carbon dioxide and producing materials with potential for pharmaceutical development (Geldenhuys & MacDevette 1989; Dajoz 2000; DWAF unpublished reports a & b). In addition, forests are a valuable tourist attraction and the simple rarity of the forests in South Africa increases their importance (Adamson 1938; Rutherford & Westfall 1994; Low & Rebelo 1996).

Despite the products and services derived from forests, they have been exploited heavily in the past, both by rural communities and for commercial timber consumption (Geldenhuys *et al.* 1986). During the nineteenth and early twentieth centuries valuable timber such as stinkwood *Ocotea bullata* (Burch.) Baill. and Outeniqua yellowwood *Podocarpus falcatus* (Thunb.) R. Br. Ex Mirb. was removed in great quantities from the forests (Geldenhuys & MacDevette 1989; Low & Rebelo 1996). Several Afromontane tree species make

excellent building materials and highly desirable furniture woods, resulting in their exploitation (Meadows 1985). In addition, there was a great demand for timber for the mining industry that caused a large amount of indiscriminate cutting (Adamson 1938). Forests were cleared for agriculture, despite the fact that the mountainous nature of most forested land renders it of little cultivation value, and grazing by cattle opened up the forest interior (Adamson 1938; Geldenhuys *et al.* 1986). Many forests today, although in advanced stages of recovery, still show signs of the past exploitation (Geldenhuys & MacDevette 1989) and human-induced disturbances will have long-term impacts on forest species composition (von Maltitz *et al.* 2003).

Humanity continues to exert pressure on the environment, and this stress is increasing (Geldenhuys & Knight 1989). South African indigenous forests face mounting pressure from humans because of the needs of the surrounding rural communities, tourism and timber industries. Specific species of forest trees continue to be exploited for timber (Low & Rebelo 1996) and this remains the main form of direct utilization of forests (Rutherford & Westfall 1994). Other forest species are used for muthi, or traditional medicines, and food is gathered from forests (Geldenhuys & MacDevette 1989; Low & Rebelo 1996; von Maltitz *et al.* 2003). Forest trees are used for firewood and poles in highly populated and rural areas (Geldenhuys & MacDevette 1989; Low & Rebelo 1996). Many forests in rural areas are threatened by non-sustainable utilization (Midgley *et al.* 1997) and the increased level of their use has caused significant disturbance to the forests (Geldenhuys & MacDevette 1989). Recent demographic pressure and the associated poverty crisis are threatening the balance between indigenous forest utilization and conservation in South Africa (Seydack 1997). As a result, there are two important potential impacts: (1) the overconsumption of forest products and collapse of sustainable resource use and (2) the transformation of forest areas to non-forest due to agriculture or informal settlements (Seydack 1997).

Plantation forestry is also affecting the health and future of the indigenous forests in South Africa. Fast-growing alien trees were planted in forest gaps and along the margins of indigenous forests immediately after European colonization (Geldenhuys *et al.* 1986). Some indigenous forests were removed entirely to establish exotic plantations (Low & Rebelo 1996). By 1983 commercial timber plantations covered 1.1 million hectares in South Africa (Geldenhuys *et al.* 1986). Currently 1.5 million hectares, or about 1.18% of

South Africa's vegetation cover, is planted with exotic forest trees (McGeoch 2002). Although plantation forestry has relieved some of the pressure on indigenous forests (Midgley *et al.* 1997), plantations usually have less total biodiversity than indigenous forests (Burley 2002) and this is true for plants (Richardson *et al.* 1992) and birds (Armstrong & van Hensbergen 1996) in South Africa. According to Ratsirarson *et al.* (2002), indigenous forests in the Cape Peninsula National Park are 2.4 times richer in leaf-litter invertebrates than pine plantations and 1.8 times richer than eucalypt plantations. Plantation forestry can also directly affect nearby indigenous forests. Plantations of pines and eucalypts use large quantities of water, disturb hydrological processes and can threaten indigenous forests' water supply (Meadows 1985; Low & Rebelo 1996). They also exclude fires, which can change disturbance regimes and energy flows in the area (Armstrong *et al.* 1998). Improper preparation and harvesting practices can compact soil, increase erosion and cause soil nutrient loss (Grey 1989), all of which may impact nearby forests. Forestry with exotic species is affecting areas set aside for conservation and water production (Richardson 1998), including indigenous forests and grasslands.

South African forests are also threatened by the invasion of non-indigenous species. At least 36 species of exotic invader plants have been recorded in South African forest margins and gaps and under closed forest canopies (Geldenhuys *et al.* 1986). Widespread South African forest invaders include *Acacia melanoxylon* R. Br., *A. mearnsii* De Wild. and *Psidium guajava* L. (Geldenhuys *et al.* 1986; Low & Rebelo 1996). Alien plants often form dense stands in forests that inhibit the establishment of indigenous species, can decrease diversity and can increase fire hazards (Geldenhuys *et al.* 1986).

Because of the various misuses, forests have become increasingly fragmented in recent times (Midgley *et al.* 1997). Forests are now considered one of the most vulnerable of South Africa's vegetation types (von Maltitz *et al.* 2003).

6.1.2 South African forest conservation

Measures have been taken to help curtail the destruction of South Africa's forests. Forests are now largely controlled and indigenous timber is only harvested on a commercial scale from the southern Cape forests (Geldenhuys *et al.* 1986, Midgley *et al.* 1997). Many forests are safe from exploitation due to their isolation in remote areas and a significant

proportion of forests have already been conserved (Table 6.1). However, proclaiming isolated stands of forest may not be enough to ensure their health and functioning (Low & Rebelo 1996).

Scientists recognize that effective conservation of South African forests is complicated. The distribution, small size and fragmented nature of forests create special problems for their conservation and management. According to Seydack (1997), the challenge of indigenous forest management in South Africa is characterised by three main features: (1) indigenous forests represent a scarce resource, (2) multiple interests or demands apply to these forests and (3) resource demands are increasing due to demographic pressure. The fact that a significant percentage of South African forests is conserved does not imply that the ecological processes that maintain forest biodiversity and ecosystem functioning are fully protected and operational (Midgley *et al.* 1997), nor that forests are safe from human exploitation. Conservation of the protected, yet isolated, forest patches depends upon the preservation of species within the forests and the ecosystem processes that operate within and between the islands (Midgley *et al.* 1997). Ecologists cannot wisely prioritize conservation efforts without first identifying key species and processes (Barbier *et al.* 1994).

Table 6.1: Area and proportion of different forest types conserved in southern Africa (Low & Rebelo 1996).

<i>Forest type</i>	<i>Area (km²)</i>	<i>Proportion conserved (%)</i>
Afromontane forest	5877	17.64
Coastal forest	946	9.51
Sand forest	354	44.62

Public authorities own the largest proportion of indigenous forests and the largest forests in South Africa (Geldenhuys & MacDevette 1989). In terms of part 2 of the National Forests Act (Act No. 84, 1998), the Minister through the Department of Water Affairs and Forestry is (1) obliged to monitor the management of forests in South Africa, with reference to amongst other things, the level of maintenance and development of forest resources, biological diversity in forests, the health and vitality of forests, the productive functions of forests, the protective and environmental functions of forests and the social functions of forests and (2) responsible for the management of declared protected areas, i.e. to manage

the protected area in a manner consistent with the purpose for which it was established (Geldenhuys & Venter 2002).

6.1.3 Limpopo Province forest conservation at present

The greatest contemporary threats to Limpopo Province forests are anthropogenic in origin. Many people live in the rural areas surrounding forests and they continually utilize forest products. Plants, bark and wood are removed for fuel, building materials, woodcarving, basket making and traditional medicines, domestic animals are grazed in forests and forest animals are poached for food (Venter 2000; Geldenhuys & Venter 2002; Forbes 2003; von Maltitz *et al.* 2003; DWAF unpublished reports a & b). There is also a demand for recreation within the forests, which necessitates the establishment of hiking trails and picnic sites.

According to von Maltitz *et al.* (2003), there are about 19 000 hectares of Northern Mistbelt Forest in Limpopo Province and 61% of it is conserved. Just under half of this conserved area is on DWAF land (von Maltitz *et al.* 2003). All indigenous forests protected by DWAF are allocated a management class, which identifies the eventual management objective (van Dijk 1987, Table 6.2). Four forests sampled during this study are classified as ‘Bioreserves,’ which are protected and managed strictly to conserve nature, and are selected to maintain representative samples of habitats, ecological diversity and genetic resources (DWAF unpublished reports a & b). The remaining seven sampled forests are classified as ‘Nature Reserves,’ which are recognized for high biodiversity value, but circumstances do not allow the exclusion of extractive utilization (DWAF unpublished reports a & b). Bioreserves and Nature Reserves are categories used to protect areas that do not qualify in terms of size, wildness or atmosphere as wilderness areas (Scott, D.F. 1987).

Table 6.2: Management classifications of Limpopo Province forests protected by DWAF (DWAF unpublished reports a & b).

<i>Forest</i>	<i>Primary Classification</i>	<i>Secondary Classification</i>
Hanglip	Nature Reserve	High intensity recreational use, Socio-cultural use
Roodewal	Nature Reserve	Conservation-constrained sustainable utilization
Goedehoop	Bioreserve	Socio-cultural use
Ratombo	Bioreserve	
Entabeni	Bioreserve	Socio-cultural use
Thathe Vondo	Nature Reserve	High intensity recreational use, Low intensity recreational use, Socio-cultural use
Grootbosch	Bioreserve	
New Agatha	Nature Reserve	
Swartbos	Nature Reserve	Low intensity recreational use
Baccarat	Nature Reserve	Protection due to ecological fragility
Forest Glens	Nature Reserve	Low intensity recreational use

Concise management plans have not yet been drafted for these protected areas, but it is the intention of DWAF to develop management plans for the existing Nature Reserves and Bioreserves in Limpopo Province (Geldenhuis & Venter 2002). To enable the Indigenous Forest Management Division of DWAF to implement wise sustainable forest management policies in the province, forest biodiversity information must be gathered and incorporated into guidelines (Geldenhuis & Venter 2002). This study provides some of that information.

6.2 LIMPOPO PROVINCE FOREST INVERTEBRATES

6.2.1 Invertebrate species diversity – major findings

Invertebrate species diversity was investigated in Chapter 3. Species richness, diversity and evenness were calculated for each region, forest and individual target group and absolute measures were also presented. Introduced invertebrate species were considered and the variables that affect indigenous target group species richness were addressed.

- In terms of target group species richness, diversity and evenness, there were no important differences between the Soutpansberg and Drakensberg regions.

- There were significant differences between the invertebrate target group richness, diversity and evenness of individual forests. Absolute measures of richness, diversity and evenness are cumulative measures and they most accurately reflect the true characteristics of total forest fauna.
- The figures presented in this chapter consider all species equally, although some groups may comprise more unique, specialized or endemic species (Chapter 4). When individual target groups were analyzed, forest ranking varied dramatically.
- When compared to other forest sites in South Africa, the invertebrate species richness of Limpopo Province forests is moderate to high.
- Because the richness, diversity and evenness measures presented in this chapter do not consider species identity, these results are of limited value to conservation and management.
- The factors that affect total target group richness in Limpopo Province forests could not be determined. With the exception of spiders, the variables that influence individual target group richness could not be identified. Spider richness is significantly affected by forest altitude, which causes variations in vegetation structure.
- Introduced molluscs and earthworms are present in Limpopo Province forests. However, there was no evidence to suggest that these affect indigenous faunas.
- Although the field species accumulation curves show that most groups were sampled completely, the randomized species accumulation curves indicate that more target species are likely to be found with additional sampling.

6.2.2 Invertebrate communities, distribution and biogeography – major findings

Distributions of Limpopo Province forest invertebrates were investigated in Chapter 4. Similarity analyses were used to compare forests and to determine affinities between forested regions. Patterns of endemism were also explored.

- Similarities in species composition were most marked between Limpopo Province forests of the same forest subtype and in the same region.
- Following current biogeographic theory, close forests were generally more similar in terms of invertebrate species composition than forests further away.
- Each forest and forest subtype had unique species. A total of 67 target group species were unique to a single forest patch and 80 target group species were

unique to a single forest subtype. Unique families were also found in single forest patches (13 families) and forest subtypes (16 families).

- Results suggest that Limpopo Province invertebrate assemblages are likely the result of northward radiations from Pleistocene forest refugia.
- The arid Limpopo River valley is a barrier to invertebrate species' radiations, but its overall effectiveness is questionable.
- Limpopo Province forests support high numbers of endemic species. A total of 47 endemic target group species (all levels) were sampled. Some target groups have more endemics than others do and levels of endemism vary according to group. This is probably due to differences in dispersal ability, speciation rate, tolerance of environmental conditions outside of forests and degree of sampling.
- Few data have been published on patterns of invertebrate endemism in South African forests. Comparisons that were possible suggest that, by South African terms, Limpopo Province forests do not support exceptional numbers of invertebrate endemics.
- Invertebrate species endemism in Limpopo Province forests is influenced by distance from likely sites of Pleistocene forest refugia, so it is likely that forest endemism is a product of historical processes.

6.2.3 Assessment of biodiversity surrogates – major findings

Potential surrogates for invertebrate richness and distributions were assessed in Chapter 5.

- No single invertebrate taxon can be used to indicate the total target invertebrate species richness of Limpopo Province forests, nor can plant or bird species.
- Significant positive correlations in richness between taxa are rare. With the exception of millipedes and centipedes, there were no significant correlations between the richness of individual invertebrate target groups, plants or birds in Limpopo Province forests.
- Invertebrate family and genus levels can be used as accurate indicators for species in Limpopo Province forests, but patterns in species richness can be masked and important site assets such as endemism may be overlooked. Therefore, this method is not recommended when inventorying for conservation prioritization.
- The morphospecies approach overestimated invertebrate richness and sorting mistakes varied according to taxon. This approach is not recommended.

- Vegetation classification accurately suggested some patterns in invertebrate species distribution in Limpopo Province forests. However, it should not be used for conservation planning since many site-restricted invertebrate species may be overlooked.
- Formal species identification should be used when surveying invertebrates for conservation and management.

6.2.4 Additional information

New species discoveries

It is not unusual to discover new invertebrate species (New 1998), especially in forests (Stork 1997). In the present study, a total of nine new species were identified by specialists, including one earthworm, five millipede, one centipede and two mollusc species. A further nine species were identified as ‘cf’ that could also be new species. Although all of these species will need further specialist investigation to confirm their status, they represent an important proportion (7%) of all indigenous target group species sampled. In addition, many spider, millipede and mollusc species could not be identified and were only assigned species numbers. The large numbers of insects and other arthropods collected in pitfall traps may also contain numerous undescribed species.

The most unexpected discovery was the new centipede species. According to Lawrence (1955a), it is unlikely that many new centipede species remain to be discovered in South Africa. However, the new *Lamyctes* species is not described and does not appear in any existing keys (G. Edgecombe 2002, pers. comm.), despite its presence throughout the study area in large numbers. There may even be additional new centipede species in Limpopo Province forests, since geophilomorphs could not be identified beyond the order level.

Perhaps the most important new species discovered in this study was the carnivorous slug *Chlamydephorus* sp. n. This species belongs to the Chlamydephoridae, one of five southern relict families and southern Africa’s only endemic terrestrial molluscan family (Herbert 1997). This new species represents the first record of the genus in Limpopo Province and will add much to the distribution data for this unique group. According to Herbert (1997), the Chlamydephoridae are vulnerable and are important in conservation terms since they primarily inhabit undisturbed areas, they are rarely abundant, species

distributions are likely to be restricted and discontinuous, they have specialized feeding habits and they occupy a high tropic level.

Special species

Red Data Books and the Red List are records of the more evident elements of biota that are known to be threatened or extinct, and are produced to focus attention on species of conservation concern by assessing the risk of species extinction (Ferrar 1989; M. L. Hamer 2003, pers. comm.). They also attempt to establish the nature and extent of decline and to suggest priorities for conservation, monitoring and research (Ferrar 1989). Red Data Books are used to list nationally or regionally threatened species while the Red List includes those species that are globally threatened (M. L. Hamer 2003, pers. comm.).

With the exception of butterflies (Henning & Henning 1989), no Red Data Books have been compiled for South African invertebrate taxa. A search of the International Union for Conservation of Nature and Natural Resources (IUCN) Species Survival Commission's Red List website revealed that less than a third of all South African Red Listed animal species are invertebrates (IUCN 2002, Figure 6.1). Most of the South African invertebrate species listed belong to the order Lepidoptera (butterflies and moths), which account for about 57% of all South African invertebrates listed (IUCN 2002). With the exception of terrestrial molluscs (six species listed, none sampled in the present study), all of the invertebrate taxa targeted during the present study are absent from the South African list (Hamer & Slotow 2002, IUCN 2002).

The formal publication of lists of species considered to be threatened, such as Red Data Books, inevitably raises serious problems relating to a shortage of information (McIntyre 1992). According to Herbert (1998) the absence of Red Listed invertebrate species from South Africa is undoubtedly an incorrect representation of the true situation and reflects the lack of knowledge and inadequate sampling of invertebrate groups. Hamer & Slotow (2002) estimate that at least 345 species of South African millipedes would potentially be classified as 'Critically Endangered' as a result of their small distribution ranges. Clearly, Red Data Books and the IUCN Red List do not reliably portray South African threatened invertebrates or decline.

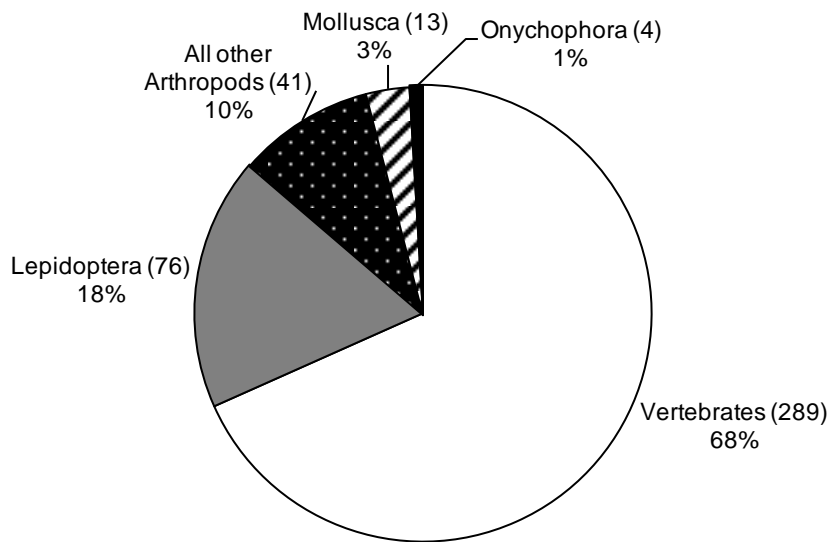


Figure 6.1: The proportion (and number) of Red Listed invertebrate species, including terrestrial, marine and freshwater species, as a percentage of all South African animal species listed (IUCN 2002).

Although no invertebrate species sampled in Limpopo Province forests was found in Red Data Books or on the Red List, many species of special importance were sampled during this study. A large proportion of species were endemic at various levels (Chapter 4) and many of these, particularly the site endemics, would qualify to be Red Listed under the current IUCN criteria. For example, three species of *Chlamydephorus* have already been Red Listed for South Africa (IUCN 2002) and *Chlamydephorus* sp. n. sampled in the present study would certainly qualify to be listed as well. In addition to the endemic species, many other ‘special species’ were sampled, which include: (1) species identified by specialists as rare and therefore potentially threatened, (2) species that occur in the study area at the northern range limit of the species and (3) species whose new locality in Limpopo Province forests has made an important contribution to its known distribution. Some non-target group endemics were also sampled that were not included in the Chapter 4 analysis. These ‘special species’ sampled in this study are given in Table 6.3.

Table 6.3: 'Special species' sampled in Limpopo Province forests. New species, potentially new species and target group endemics are not included. The categories are defined as follows: Important record = the sampled locality is new and contributes to the species' distribution. Northernmost record = species presence in the study area was previously known and is the northernmost extent of the species' distribution. Endemic = non-target group species or subspecies that is endemic. Rare = species rare in South Africa. The following abbreviations are used: SPB = Soutpansberg, DKB = Drakensberg, LP = Limpopo Province, KZN = KwaZulu-Natal, GP = Gauteng Province, MP = Mpumalanga Province, SA = South Africa.

Taxon	Species	Category	Comments	Reference
Millipedes	<i>Gnomeskelus cygniceps</i>	Important record	Previously known only from SPB, sampled in DKB	Hamer 1998
	<i>Gnomeskelus krugeri</i>	Important record	Previously known only from Kruger National Park, sampled in SPB	Hamer 1998
Molluscs	<i>Uloidesmus propinquus</i>	Important record	Previously known only from DKB, sampled in SPB	Hamer 1998
	<i>Patinatus capucinus</i>	Important record	Previously known only from DKB, sampled in SPB	Hamer 1998
	<i>Centrobolus inyanganus</i>	Important record	Previously known only from Inyanga Zimbabwe	Hamer 1998
	<i>Sphaerothertium dorsale</i>	Important record	Previously known only from E. Cape, W. Cape and KZN	Hamer 1998
Spiders	<i>Doratogonus herberti</i>	Important record	Previously known only from SPB, sampled in DKB	Hamer 1998
	<i>Edvardia dimera</i>	Important record	First record of species in LP, northernmost record of species	D.G. Herbert 2002, pers. comm.
Insects	<i>Araneus nigroquadratus</i>	Important record	Previously known only from GP, KZN and MP within SA	A.S. Dippenaar-Schoeman 2002, pers. comm.
	<i>Argiope levii</i>	Important record	Previously known only from Lake Sibayi KZN within SA	A.S. Dippenaar-Schoeman 2002, pers. comm.
	<i>Allothele malawi</i>	Rare		A.S. Dippenaar-Schoeman 2002, pers. comm.
	<i>Azania lobus lawrenzei</i>	Important record	Previously known only from Mariepskop LP	A.S. Dippenaar-Schoeman 2002, pers. comm.
	<i>Cheiramiona clavigera</i>	Important record	Previously known only from KZN and W. Cape	A.S. Dippenaar-Schoeman 2002, pers. comm.
	<i>Crozetus rhodesiensis</i>	Rare		A.S. Dippenaar-Schoeman 2002, pers. comm.
	<i>Cyphalonotus larvatus</i>	Important record	Previously known only from KZN, GP and Makalali LP within SA	A.S. Dippenaar-Schoeman 2002, pers. comm.
	<i>Hyptiotes akermani</i>	Important record	Previously known only from KZN	A.S. Dippenaar-Schoeman 2002, pers. comm.
	<i>Leucauge argyrescens</i>	Important record	Previously known only from KZN and Seychelles	A.S. Dippenaar-Schoeman 2002, pers. comm.
	<i>Leucauge levanderi</i>	Important record	Previously known only from KZN within SA	A.S. Dippenaar-Schoeman 2002, pers. comm.
Insects	<i>Mimeis cornutus</i>	Important record	Previously known only from KZN	A.S. Dippenaar-Schoeman 2002, pers. comm.
	<i>Pachynatha teleupi</i>	Rare		A.S. Dippenaar-Schoeman 2002, pers. comm.
	<i>Xevioso lichmadina</i>	Rare		A.S. Dippenaar-Schoeman 2002, pers. comm.
	<i>Parachilota davenda</i>	Rare		A.S. Dippenaar-Schoeman 2002, pers. comm.
	<i>Parachilota hutchinsoni</i>	Important record	Species and genus not known further north	Pickford 1937
	<i>Tritogenia silvicola</i>	Northernmost record	Species and genus not known further north	Pickford 1937
	<i>Calyptomymex brunneus</i>	Northernmost record	Genus is probably not known further north	Plisko 1997
	<i>Tetramorium grassii</i>	Important record	Previously known from KZN and Vumba Zimbabwe	H. Robertson 2002, pers. comm.
	<i>Papilio ophicephalus entabeni</i>	Endemic	New northernmost record of the species	H. Robertson 2002, pers. comm.
	<i>Temnora zanthus zanthus</i>	Endemic	Species endemic to South Africa	H. Robertson 2002, pers. comm.
Insects	<i>Syritysyrphus opacea</i>	Important record	Subspecies endemic to the Soutpansberg	Pringle et al. 1994
		Endemic	Subspecies endemic to South Africa	Pringle et al. 1994
Insects		Important record	Previously known only from the E. Cape and Vumba Zimbabwe	W. Barkemeyer 2002, pers. comm.
		Important record		

6.3 CONSERVATION OF LIMPOPO PROVINCE FORESTS

6.3.1 Why conserve Limpopo Province forests?

In addition to the uses and contributions of South African forests as described in Section 6.1.1, Limpopo Province forests are important for the conservation of species belonging to many taxa. The present study has shown that Limpopo Province forests support valuable assemblages of invertebrates, including unique, endemic and threatened species. These forests are also botanically interesting and contain a large number of endemic plant species and species whose presence is disjunct or is at the northern or southern range limit (Geldenhuys & Venter 2002). In term of vertebrates, Limpopo Province forests support a variety of threatened species (Forbes 2002). These include the rare samango monkey *Cercopithecus mitis* Wolf, 1822, the red duiker *Cephalophus natalensis* A. Smith, 1834 and the giant rat *Cricetomys gambianus* Waterhouse, 1840 (Smithers 1986). Five reptile species are endemic to Limpopo Province forests, including the black whitelipped snake *Amblyodipsas microphthalma nigra* Bianconi, 1850, the Woodbush flat gecko *Afroedura pondolia multiporis* Hewitt 1925, the vulnerable Woodbush legless skink *Acontophiops lineatus* Sternfeld 1919, the near threatened Soutpansberg rock lizard *Lacerta rupicola* (FitzSimons, 1933) and the near threatened Soutpansberg flat lizard *Platysaurus relictus* Broadley, 1976 (Branch 1988; IUCN 2002). Five threatened forest bird species have been recorded in Limpopo Province forests, including the endangered cape parrot *Poicephalus robustus* Gmelin, 1788, the vulnerable Delegorgues pigeon *Columba delegorguei* Delegorgue, 1847, and the near threatened African broadbill *Smithornis capensis* Smith, 1840, orange thrush *Zoothera gunneyii* Hartlaub, 1864 and crowned eagle *Stephanoaetus coronatus* Linnaeus, 1766 (Barnes 2000; Forbes 2002).

6.3.2 Which forests should be conserved in Limpopo Province?

Human and financial resources are not sufficient to protect and manage all diversity and it is therefore essential that available skills and funds be directed to sites of the highest conservation priority (Huntley 1988). Conservation prioritization requires information on the current distribution and status of biodiversity (Armstrong 2002), so selection is often made using plants and vertebrates. However, planning based solely on these data is unlikely to conserve a significant proportion of other diversity (Hamer & Slotow 2002).

Invertebrates do not have the same requirements as long-lived plants and vertebrates and should be included in planning and prioritization of conservation areas.

Conservation prioritization and area selection can be based on various criteria, including the species richness or diversity present, levels and amounts of endemism, the rarity or threatened status of species or habitat types, habitat patch size and degree of disturbance or destruction (Dony & Denholm 1985; Brown 1991; Hawksworth & Kalin-Arroyo 1995; Miller *et al.* 1995; Spellerberg 1996b; New 1998; Hamer & Slotow 2002). For example, an area with higher diversity may be considered more important than one with lower diversity (Hawksworth & Kalin-Arroyo 1995).

Limpopo Province forest patches can be ranked for invertebrate conservation according to such criteria. However, forests rank differently depending upon the aspect of invertebrate biodiversity considered (Table 6.4). For example, Roodewal would be a priority forest patch if conserving for unique species or total invertebrate species richness. However, it ranks the lowest for number of forest endemics. Similarly, Swartbos is a low priority according to total invertebrate species richness, but contains a relatively high number of forest endemics.

Larger habitat patches usually contain greater habitat diversity (Saunders *et al.* 1991) and therefore greater biodiversity. They also tend to support larger and more persistent populations (Saunders *et al.* 1991; Fahrig & Merriam 1994) and minimize edge effects (Primack 2000). However, conservation prioritization based solely upon forest size would not effectively protect forest invertebrate species in Limpopo Province. Grootbosch, which is more than 100% larger than any other forest patch studied, only contains about 28% of all indigenous invertebrate species sampled. Even if all forests over 1000 hectares were conserved (Grootbosch, Thathe Vondo, Entabeni and New Agatha), only about 58% of indigenous invertebrate species sampled would be protected. Large forest patches are important, but small patches also support important invertebrate (this study) and vertebrate (Forbes 2002) diversity. According to the results of this study, no single forest can be excluded from conservation if all aspects of diversity are considered.

Table 6.4: Differential ranking of forests for conservation based on six individual criteria. Forests are listed in descending order. Only indigenous target group invertebrate species were considered. Values for each category are indicated by parentheses.

Total richness (S_{ab})	Total diversity ($N1_{ab}$)	Unique species	Forest endemics	Percent of total S_{ab} *	Size (ha)
Entabeni (42)	Ratombo (21.04)	Roodewal (16)	Entabeni (9)	Entabeni (30)	Grootbosch (4625)
New Agatha (42)	Entabeni (19.31)	Ratombo (12)	New Agatha (9)	New Agatha (30)	Thathe Vondo (2000)
Roodewal (41)	Hanglip (16.28)	New Agatha (7)	Baccarat (9)	Roodewal (30)	Entabeni (1393)
Baccarat (39)	Goedehoop (15.32)	Goedehoop (5)	Grootbosch (8)	Baccarat (28)	New Agatha (1255)
Grootbosch (38)	Forest Glens (15.10)	Swartbos (5)	Swartbos (7)	Grootbosch (28)	Roodewal (612)
Hanglip (38)	Baccarat (11.44)	Baccarat (5)	Forest Glens (7)	Hanglip (28)	Hanglip (354)
Ratombo (38)	New Agatha (11.23)	Entabeni (4)	Thathe Vondo (6)	Ratombo (28)	Baccarat (309)
Forest Glens (35)	Grootbosch (9.72)	Grootbosch (4)	Ratombo (6)	Forest Glens (25)	Goedehoop (243)
Goedehoop (34)	Roodewal (9.51)	Hanglip (3)	Hanglip (6)	Goedehoop (25)	Ratombo (171)
Thathe Vondo (33)	Swartbos (8.60)	Thathe Vondo (3)	Goedehoop (5)	Thathe Vondo (24)	Forest Glens (71)
Swartbos (33)	Thathe Vondo (5.76)	Forest Glens (3)	Roodewal (2)	Swartbos (24)	Swartbos (52)

* Percentage of total Limpopo Province invertebrate species richness represented in forest.

The challenge of conservation prioritization of Limpopo Province forests is compounded when integrating additional taxa such as plants and vertebrates. For example, Forbes (2002) identified Baccarat, Grootbosch (Woodbush) and Swartbos as important for the conservation of the endangered Cape parrot, the blackfronted bushshrike *Telophorus nigrifrons* Reichenow, 1896 and the samango monkey and Entabeni, Goedehoop, Grootbosch (Woodbush), Swartbos and Baccarat as important for the protection of the near threatened orange thrush. Clearly, no single taxon or criterion can identify every valuable area. All possible criteria and taxa must be considered if prioritizing forests for conservation.

6.3.3 How should we conserve forests in Limpopo Province?

Forest conservation in South Africa has two major facets: (1) maintenance of the components and critical processes within a forest and (2) maintenance of gene flow between different forests (Geldenhuys & MacDevette 1989). The majority of Limpopo Province forests and all forests sampled in the present study are already protected by DWAF, which is responsible for maintaining diversity within forests. However, management classifications indicate that at least some forests are to be utilized and conservation must not exclude people from their traditional ways of life (New 1998). Because sustainable use of forests requires that their fauna be effectively conserved (Low & Rebelo 1996), any utilization must be carefully evaluated to determine if it may impact forest species and compromise facet (1). Passive (picnicking) and active (hiking) recreation in forests, for example, can be reasonably controlled and, if managed properly, have minimal impact on the forests. In contrast, activities such as grazing, firewood collection and removal of plants could potentially impact invertebrate populations. Dead and decaying wood, in particular, is of great importance to invertebrate conservation (Kirby 1992; McComb & Lindenmayer 1999). Internal forest fragmentation by roads and wide paths should also be avoided (Primack 2000).

Because Limpopo Province forests are patchily distributed, gene flow between forests is not easy to maintain. Without gene flow, small isolated populations can lose genetic variability and evolutionary flexibility and can experience inbreeding or outbreeding depression (Primack 2000). Corridors, or dispersal routes, are important to the long-term viability of populations within fragmented or naturally patchy habitats because they link

separate, isolated populations (Norton 1999). Corridors are generally believed to enhance biotic movement and facilitate gene flow, maintain or increase patch richness, supply additional foraging areas, provide refuges during disturbances, allow for the colonization of suitable sites and enhance the aesthetic appeal of the landscape (Saunders *et al.* 1991; Stewart & Hutchings 1996; Primack 2000). Even if they are not essential for a species, corridors increase the probability of movement and long-term species survival (Miller *et al.* 1995). Although it has also been suggested that corridors may negatively impact populations (Stewart & Hutchings 1996), there is no evidence to confirm that this applies to corridors preserved for conservation (Beier & Noss 1998).

Dispersal corridors for Limpopo Province forest biota include riparian and valley forests, thickets and bush-clumps, which link forest patches and coastal and montane forest types (Geldenhuys & MacDevette 1989). Forest patches themselves can also serve as ‘stepping stones’ and form part of a dispersal route between two other patches (Fahrig & Merriam 1994), highlighting the importance of smaller forest patches.

Many of the vital forest species’ dispersal routes that exist in South Africa, including small forest patches and corridors, are not protected (Geldenhuys & MacDevette 1989) and this is the present situation in Limpopo Province. Areas outside of formally conserved areas, such as dispersal corridors and adjacent vegetation, are an important component of the conservation network (Miller *et al.* 1995) and must also be protected in Limpopo Province to ensure the continued survival of forest species. Effective corridors must be wide enough to contain a significant interior area (Miller *et al.* 1995), so narrow corridors must be rehabilitated and new corridors may need to be created. Further, Limpopo Province timber plantation owners should be encouraged to include conservation as a secondary priority in management and to enhance biodiversity within plantations, since this could increase the area of conservation management, protect more species and decrease the effects of forest isolation (Moore & Allen 1999; Primack 2000).

6.4 CONCLUSION

This study has shown that there is no substitute for formal species identification in invertebrate biodiversity studies, especially when results are used for conservation and

management purposes. Conservation of Limpopo Province forests is vital for many reasons, including the preservation of valuable invertebrate communities. Conservation prioritization of forests is largely dependent upon the facets of biodiversity that are deemed important, such as endemism, rarity or total diversity, and all aspects should be considered. No forest sampled in this study can be considered insignificant and each is worthy of conservation. Effective forest conservation and management is dependent upon the protection of forests of varying patch size, careful evaluation and control of utilization and the establishment and maintenance of corridors linking isolated forest patches.

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Appendix 1: List of all specimens sampled in Limpopo Province indigenous forests. The method(s) used to collect the specimens are indicated. Q = Quadrat sampling, T = Transect sampling, P = Pitfall sampling, O = Other. Introduced species are indicated by (*). Scholtz & Holm (1985) Insecta classification has been followed.

PHYLUM ANNELIDA

CLASS OLIGOCHAETA

<i>Order</i>	<i>Family, genus, species</i>	<i>Author</i>	<i>Method</i>
Haplotaxida	Acanthodrilidae:		
	<i>Dichogaster affinis</i> *	(Michaelsen, 1890)	Q
	<i>Dichogaster bolau</i> *	(Michaelsen, 1893)	Q
	<i>Dichogaster saliens</i> *	(Beddard, 1893)	Q
	<i>Parachilota bavenda</i>	Pickford, 1937	Q, P
	<i>Parachilota hutchinsoni</i>	Pickford, 1937	Q, P
	<i>Parachilota</i> sp. n.		Q
	<i>Parachilota</i> sp.		Q
	Glossoscolecidae:		
	<i>Pontoscolex corethrurus</i> *	(Muller, 1857)	Q
	Lumbricidae:		
	<i>Aporrectodea rosea</i> *	(Savigny, 1826)	Q
	<i>Dendrobaena octaedra</i> *	(Savigny, 1826)	Q
	<i>Dendrodrilus eseni</i> *	(Levinsen, 1884)	Q
	<i>Dendrodrilus rubidus</i> *	(Savigny, 1826)	Q, P
	<i>Octolasion lacteum</i> *	(Oerley, 1885)	Q, P
	Megascolecidae:		
	<i>Amyntas diffringens</i> *	(Baird, 1896)	Q, P
	<i>Amyntas minimus</i> *	(Horst, 1893)	Q, P
	<i>Amyntas rodericensis</i> *	(Grube, 1879)	Q
	Microchaetidae:		
	sp.		Q, P
	<i>Tritogenia silvicola</i>	Plisko, 1997	Q
	<i>Tritogenia turneri</i>	Plisko, 1997	Q

PHYLUM ARTHROPODA

CLASS COLLEMBOLA

<i>Order</i>	<i>Family, genus, species</i>	<i>Author</i>	<i>Method</i>
unknown			P

PHYLUM ARTHROPODA

CLASS DIPLURA

<i>Order</i>	<i>Family, genus, species</i>	<i>Author</i>	<i>Method</i>
Diplura	Japygidae		P

PHYLUM ARTHROPODA

CLASS INSECTA

<i>Order</i>	<i>Family, genus, species</i>	<i>Author</i>	<i>Method</i>
Archaeognatha	Meinertellidae		P
Ephemeroptera			P
Odonata	Coenagrionidae		O
	Platycnemididae		O
Blattodea	Blattellidae		P
	Blattidae		P
Isoptera			P
Orthoptera	Gryllidae		P
	Stenopelmatidae		P

<i>Order</i>	<i>Family, genus, species</i>	<i>Author</i>	<i>Method</i>	
Orthoptera (continued)	Tetrigidae		P	
	Tettigoniidae		P	
Dermaptera	Forficulidae		P	
	Labiduridae / Brachylabinae		P	
	Pygidicranidae		P	
Hemiptera	Cydnidae		P	
	Lygaeidae / Pachygronthinae		P	
	Lygaeidae / Rhyparochrominae		P	
Thysanoptera	Homoptera (suborder)		P	
	Phlaeothripidae		P	
Coleoptera	Carabidae		P	
	Chrysomelidae		P	
	Chrysomelidae / Cryptocephalinae		P	
	Curculionidae		P	
	Elateridae		P	
	Histeridae		P	
	Lampyridae		P	
	Nitidulidae		P	
	Scarabaeidae / Melolonthinae		P	
	Scarabaeidae / Scarabaeinae		P	
	Staphylinidae		P	
	Tenebrionidae		P	
	Hymenoptera	Braconidae		P
		Ceraphronidae		P
		Diapriidae		P
		Formicidae:		
		<i>Calyptomyrmex brunneus</i>	Arnold, 1948	P
		<i>Camponotus</i> sp.		P
		<i>Camponotus cinctellus</i>	(Gerstaecker, 1859)	P
<i>Crematogaster</i> sp.			P	
<i>Dorylus</i> sp.			P	
<i>Leptogenys</i> cf. <i>intermedia</i>		Emery, 1902	P	
<i>Monomorium</i> cf. <i>exchao</i>		Santschi, 1926	P	
<i>Myrmecaria natalensis</i>		(F. Smith, 1858)	P	
<i>Paratrechina</i> sp.			P	
<i>Pheidole</i> sp.			P	
<i>Tetramorium frenchi</i>		Forel, 1914	P	
<i>Tetramorium grassii</i>		Emery, 1895	P	
<i>Tetramorium simillimum</i>		(F. Smith, 1851)	P	
Ichneumonidae			P	
Platygasteridae			P	
Pompilidae		P		
Proctotrupidae		P		
Scelionidae		P		
Diptera	Acroceridae:			
	<i>Psilodea</i> sp.		O	
	Asilidae:			
	<i>Synolcus dubius</i>	(Macquart, 1846)	O	
	Bombyliidae:			
	<i>Philoliche aethiopica</i>	(Thunberg, 1789)	O	
	Calliphoridae		P	
	Cecidomyiidae		P	
	Chaoboridae		P	
	Conopidae		P	

<i>Order</i>	<i>Family, genus, species</i>	<i>Author</i>	<i>Method</i>
Diptera (continued)	Dolichopodidae		P
	Drosophilidae		P
	Empididae		P
	Ephydriidae		P
	Heleomyzidae		P
	Muscidae		P
	Mycetophilidae		P
	Odiniidae		P
	Phoridae		P
	Pipunculidae		P
	Sarcophagidae		P
	Simuliidae		P
	Sphaeroceridae		P
	Stratiomyidae		P
	Syrphidae:		
	<i>Syrittosyrphus opacea</i>	Hull, 1944	O
	<i>Asarkina</i> sp.		O
	Tachinidae		P
	Tephritidae		P
	Thaumaleidae		P
Tipulidae		P	
Lepidoptera	Geometridae:		
	<i>Cartaetis libyssa libyssa</i>	(Hopffer, 1857)	O
	Lycaenidae:		
	<i>Leptotes babaulti</i>	(Stempffer, 1935)	O
	Noctuidae:		
	sp.		P
	<i>Cylogramma latona</i>	(Cramer, 1779)	O
	Nymphalidae:		
	<i>Bematistes aganice aganice</i>	(Hewitson, 1852)	O
	<i>Precis (Junonia) terea elgiva</i>	(Hewitson, 18640)	O
	<i>Protogoniomorpha parhassus</i>	(Drury, 1782)	O
	<i>Bicyclus safitza safitza</i>	(Hewitson, 1851)	O
	<i>Cassionympha cassius</i>	(Godart, 1824)	O
	Papilionidae:		
	<i>Papilio dardanus cenea</i>	Stoll, 1790	O
	<i>Papilio demodocus demodocus</i>	Esper, 1798	O
	<i>Papilio echeriodes echeriodes</i>	Trimen, 1868	O
	<i>Papilio nireus lyaeus</i>	Doubleday, 1845	O
	<i>Papilio ophidicephalus entabeni</i>	Van Son, 1939	O
	Pieridae:		
<i>Leptosia alcesta inalcesta</i>	Bernardi, 1959	O	
<i>Colotus (Colotus) pallene</i>	(Hopffer, 1855)	O	
<i>Eurema (Maiva) brigitta brigitta</i>	(Stoll, 1780)	O	
<i>Eurema (Terias) hecabe solifera</i>	(Butler, 1875)	O	
Sphingidae:			
<i>Polyptychus corydoni</i>	Rothschild & Jordan, 1903	O	
<i>Temnora zanthus zanthus</i>	(Herrich-Schaffer, 1854)	O	
Psocoptera	Psocidae		P
	Peripsocidae		P
Trichoptera			P

PHYLUM ARTHROPODA
SUBPHYLUM MYRIAPODA
CLASS CHILOPODA

<i>Order</i>	<i>Family, genus, species</i>	<i>Author</i>	<i>Method</i>
Lithobiomorpha	Henicopidae:		
	<i>Lamyctes</i> sp. n.		Q, P
	<i>Paralamyctes spenceri</i>	Pocock, 1901	Q
Scolopendromorpha	Scolopendromorphidae:		
	<i>Cormocephalus multispinus</i>	(Kraepelin, 1903)	Q
	<i>Cormocephalus nitidus</i>	Porat, 1871	Q, O
	<i>Cormocephalus westwoodi dispar</i>	Porat, 1893	Q
	<i>Rhysida afra</i>	(Peters, 1855)	Q
Geophilomorpha			Q, P
Scutigleromorpha	Scutigleridae:		
	<i>Scutiglerina weberi</i>	Silvestri, 1903	Q

PHYLUM ARTHROPODA
SUBPHYLUM MYRIAPODA
CLASS DIPLOPODA

<i>Order</i>	<i>Family, genus, species</i>	<i>Author</i>	<i>Method</i>	
Polydesmida	Dalodesmidae:			
	<i>Gnomeskelus arator</i>	Lawrence, 1962	Q	
	<i>Gnomeskelus cygniceps</i>	Lawrence, 1959	Q, P	
	<i>Gnomeskelus krugeri</i>	Lawrence, 1966	Q	
	<i>Gnomeskelus</i> sp. n. 1		Q	
	<i>Gnomeskelus</i> sp. n. 2		Q, P	
	<i>Gnomeskelus</i> sp. n. 3		Q	
	<i>Gnomeskelus</i> sp. n. 4		Q	
		Gomphodesmidae:		
		<i>Ulodesmus</i> sp.		Q, P
	<i>Ulodesmus propinquus</i>	Lawrence, 1962	Q	
Spirostreptida	Odontopygidae:			
	<i>Chaleponcus</i> sp. 1		Q, P	
	<i>Chaleponcus</i> sp. 2		Q, P	
	<i>Patinatius capucinus</i>	Kraus, 1966	Q, P	
	<i>Spinotarsus</i> sp. 1		Q	
		Spirostreptidae:		
		<i>Doratogonus barbatus</i>	Hamer, 2000	O
	<i>Doratogonus herberti</i>	Hamer, 2000	Q, O	
	<i>Doratogonus rugifrons</i>	(Attems, 1922)	O	
	<i>Orthoporoides</i> sp. 1		Q, O	
Spirobolida	Pachybolidae:			
	<i>Centrobolus inyanganus</i>	(Lawrence, 1967)	Q	
	<i>Centrobolus</i> cf. <i>transvaalicus</i>	(Lawrence, 1967)	Q	
Sphaerotheriida	Sphaerotheriidae:			
	<i>Sphaerotherium</i> cf. <i>dicrothrix</i>	Attems, 1928	Q, P	
	<i>Sphaerotherium dorsale</i>	(Gervais, 1847)	Q, P	
	<i>Sphaerotherium hanstromi</i>	Schubart 1958	Q, P	
	<i>Sphaerotherium</i> cf. <i>mahaïum</i>	Schubart, 1958	Q, P	
	<i>Sphaerotherium</i> cf. <i>perbrincki</i>	Schubart, 1958	Q	
	<i>Sphaerotherium</i> sp. n. 1		Q	

PHYLUM ARTHROPODA
 CLASS CHELICERATA
 SUBCLASS ARACHNIDA

<i>Order</i>	<i>Family, genus, species</i>	<i>Author</i>	<i>Method</i>
Scorpiones	Buthidae		Q
Araneae	Anapidae:		
	<i>Crozetulus rodesiensis</i>	Brignoli, 1981	P
	Araneidae:		
	<i>Araneus nigroquadratus</i>	Lawrence, 1937	T
	<i>Araneus</i> sp. 1		T
	<i>Araneus</i> sp. 2		T
	<i>Argiope levii</i>	Bjorn, 1997	T, O
	<i>Caerostris sexcuspidata</i>	(Fabricius, 1793)	T
	<i>Cyclosa insulana</i>	(Costa, 1834)	T
	<i>Cyphalonotus larvatus</i>	(Simon, 1881)	T
	<i>Gasteracantha milvodes</i>	Butler, 1873	T
	<i>Gasteracantha sanguinolenta</i>	C.L. Koch, 1845	T
	<i>Gasteracantha versicolor</i>	(Walckenaer, 1842)	T
	<i>Gasteracantha</i> sp.		O
	<i>Gea</i> sp. 1		T
	<i>Isoxya tabulata</i>	(Thorell, 1859)	O
	<i>Neoscona subfusca</i>	(C.L. Koch, 1837)	T
	<i>Neoscona</i> sp.		T
	Clubionidae:		
	<i>Clubiona</i> sp.		P
	Corinnidae:		
	<i>Austrophaea</i> sp.		P
	Ctenidae:		
	sp. 1		P
	Cyatholipidae:		
	<i>Ulwembua</i> sp.		T
	Dipluridae:		
	<i>Allothela malawi</i>	Coyle, 1984	T
	Gnaphosidae:		
	<i>Echemus</i> sp.		P
	<i>Setaphis</i> sp.		P
	<i>Xerophaeus bicavus</i>	Tucker, 1923	P
	Hahniidae:		
	<i>Hahnia tabulicola</i>	Simon, 1898	P
	Linyphiidae:		
	sp.		T, P
	sp. 1		T
	sp. 2		P
	sp. 3		T
	<i>Meioneta</i> sp.		P
	<i>Microlinyphia sterilis</i>	(Pavesi, 1883)	T
	<i>Ostearius melanopygius</i>	(O.P. Cambridge, 1879)	T
	Liocranidae:		
	sp.		P
	<i>Pronophaea</i> sp.		P
	<i>Rhaeboctesis</i> sp.		P
	Lycosidae:		
	sp.		P
	sp. 1		P
	sp. 2		P
	<i>Trabae</i> sp.		P

<i>Order</i>	<i>Family, genus, species</i>	<i>Author</i>	<i>Method</i>
Araneae (continued)	Mimetidae:		
	<i>Mimetus cornutus</i>	Lawrence, 1947	T
	Miturgidae:		
	<i>Cheiramiona clavigerum</i>	(Simon, 1897)	P
	<i>Griswoldia</i> sp.		P
	<i>Syrisca</i> sp.		P
	Nemesiidae:		
	sp.		P
	<i>Hermacha</i> sp.		P
	<i>Pionothele</i> sp.		P
	Nesticidae:		
	sp.		T
	Orsolobidae:		
	<i>Azanielobus lawrenzei</i>	Griswold & Platnick, 1987	P
	Pholcidae:		
	<i>Smeringopus</i> sp. 1		T
	<i>Smeringopus</i> sp. 2		T
	Phyxelididae:		
	<i>Xevioso lichmadina</i>	Griswold, 1990	P
	Salticidae:		
	<i>Euophrys</i> sp.		T, P
	<i>Habrocestrum</i> sp.		T
	<i>Habrocestrum</i> sp. 1		P
	<i>Habrocestrum</i> sp. 2		P
	Tetragnathidae:		
	<i>Leucauge argyrescens</i>	Benoit, 1978	T
	<i>Leucauge decorata</i>	(Blackwall, 1864)	T
	<i>Leucauge levanderii</i>	(Kulczynski, 1901)	T
	<i>Leucauge</i> sp. 1		T
	<i>Meta</i> sp. 1		T
	<i>Meta</i> sp. 2		T
	<i>Nephila pilipes</i>	(Fabricius, 1793)	T
	<i>Pachygnatha leleupi</i>	Lawrence, 1952	T, P
	Theridiidae:		
	<i>Achaeearanea</i> sp. 1		T
	<i>Argyrodes</i> sp.		T
	<i>Coleosoma</i> sp.		P
	<i>Moneta</i> sp.		P
	<i>Theridion</i> sp. 1		T
	<i>Theridion</i> sp. 2		T
	<i>Thymoites</i> sp. 1		T
	<i>Thymoites</i> sp. 2		O
	Thomisidae:		
	<i>Diaea puncta</i>	Karsch, 1884	O
	<i>Misumenops rubrodecoratus</i>	Millot, 1941	O
	<i>Runcinia aethiops</i>	(Simon, 1901)	O
	Uloboridae:		
<i>Hyptiotes ackermani</i>	Wiehle, 1964	T	
<i>Uloborus planipediis</i>	Simon, 1896	T	
Zodariidae:			
<i>Cydrela</i> sp.		P	
Opiliones			P
Acari			P

PHYLUM ARTHROPODA
 SUBPHYLUM CRUSTACEA
 CLASS MALACOSTRACA
 SUBCLASS EUMALACOSTRACA

<i>Order</i>	<i>Family, genus, species</i>	<i>Author</i>	<i>Method</i>
Amphipoda	Talitridae:		
	<i>Talitriator eastwoodae</i>	Methuen, 1913	P
Isopoda			P

PHYLUM MOLLUSCA
 CLASS GASTROPODA
 SUBCLASS PULMONATA

<i>Order</i>	<i>Family, genus, species</i>	<i>Author</i>	<i>Method</i>
Eupulmonata	Achatinidae:		
	<i>Achatina craveni</i>	Smith, 1881	Q
	Agriolimacidae:		
	<i>Deroceras</i> sp.*		Q
	Arionidae:		
	<i>Arion</i> sp.*		Q
	Cerastidae:		
	<i>Edouardia dimera</i>	(Melvill & Ponsonby, 1901)	Q
	<i>Edouardia drakensbergensis</i>	(Smith, 1877)	Q
	<i>Edouardia sordidula</i>	(Martens, 1897)	Q
	<i>Rhachistia chiradzuluensis</i>	(Smith, 18990)	Q
	Charopidae:		
	<i>Trachycystis</i> sp. 1		Q, P
	<i>Trachycystis</i> sp. 2		Q
	<i>Trachycystis</i> sp. 3		Q
	<i>Trachycystis ariel</i>	(Preston, 1910)	Q, P
	<i>Trachycystis</i> cf. <i>fossula</i>	Connolly, 1925	Q
	<i>Trachycystis</i> cf. <i>loveni</i>	(Krauss, 1848)	Q
	<i>Trachycystis</i> cf. <i>rivularis</i>	(Krauss, 1848)	Q, P
	<i>Trachycystis</i> cf. <i>subpinguis</i>	Connolly, 1922	Q
	Chlamydephoridae:		
	<i>Chlamydephorus</i> sp. n.		Q
	Clausiliidae:		
	<i>Abbadia africana</i>	(Melvill & Ponsonby, 1899)	Q
	Euconulidae:		
	<i>Afroconulus diaphanus</i>	(Connolly, 1922)	Q
	Helicarionidae:		
	<i>Kaliella barrakporensis</i>	(Pfeiffer, 1852)	Q, P
	Rhytididae:		
	<i>Nata vernicosa</i>	(Krauss, 1848)	Q
	<i>Nata viridescens</i>	(Melvill & Ponsonby, 1891)	Q
	Streptaxidae:		
	<i>Gulella harriesi</i>	Burnup, 1926	Q
	<i>Gulella inobstructa</i>	Bruggen, 1965	Q
	<i>Gulella johannesburgensis</i>	(Melvill & Ponsonby, 1907)	Q
	<i>Gulella sibasana</i>	Connolly, 1922	Q, P
	<i>Gulella viae</i>	Burnup, 1925	Q
	<i>Gulella</i> sp. n. 1		Q
	Subulinidae:		
	<i>Opeas</i> cf. <i>florentiae</i>	(Melvill & Ponsonby, 1901)	Q
<i>Opeas</i> sp. 1		Q	
<i>Opeas</i> sp. 2		Q, P	

<i>Order</i>	<i>Family, genus, species</i>	<i>Author</i>	<i>Method</i>
Eupulmonata (continued)	Urocyclidae:		
	<i>Elisolimax flavescens</i>	(Keferstein, 1866)	O
	<i>Thapsia pinguis</i>	(Krauss, 1848)	Q
	<i>Sheldonia</i> sp. 1		Q
	<i>Sheldonia</i> sp. 2		Q
	<i>Sheldonia</i> sp. 3		Q

PHYLUM MOLLUSCA

CLASS GASTROPODA

SUBCLASS PROSOBRANCHIA

<i>Order</i>	<i>Family, genus, species</i>	<i>Author</i>	<i>Method</i>
Sorbeoconcha (Mesogastropoda)	Pomatiasidae:		
	<i>Tropidophora insularis</i>	(Pfeiffer, 1852)	Q

Appendix 2: List of all collection locations for all specimens sampled in Limpopo Province indigenous forests. An (x) indicates the forest(s) where each taxon was sampled. Forest names are abbreviated as follows: HAN = Hanglip, ROD = Roodewal, GHP = Goedehoop, RAT = Ratombo, ENT = Entabeni, TV = Thathe Vondo, GRO = Grootbosch, NAG = New Agatha, SWB = Swartbos, BAC = Baccarat, FGL = Forest Glens. Bold text indicates where only higher taxon identification was possible. Introduced species are indicated by (*).

Earthworms (Class: Oligochaeta, Order: Haplotaxida)

Family	Genus, species	Soutpansberg						Drakensberg				
		HAN	ROD	GHP	RAT	ENT	TV	GRO	NAG	SWB	BAC	FGL
Acanthodrilidae	<i>Dichogaster affinis</i> *		X									
Acanthodrilidae	<i>Dichogaster bolau</i> *		X									
Acanthodrilidae	<i>Dichogaster saliens</i> *				X							
Acanthodrilidae	<i>Parachilota bavenda</i>						X			X		
Acanthodrilidae	<i>Parachilota hutchinsoni</i>				X	X		X		X	X	
Acanthodrilidae	<i>Parachilota</i> sp. n.							X				
Acanthodrilidae	<i>Parachilota</i> sp.								X			
Glossoscolecidae	<i>Pontoscolex corethrurus</i> *				X				X			
Lumbricidae	<i>Aporrectodea rosea</i> *									X		
Lumbricidae	<i>Dendrobaena octaedra</i> *									X		
Lumbricidae	<i>Dendrodrilus eseni</i> *							X				
Lumbricidae	<i>Dendrodrilus rubidus</i> *	X	X	X				X				X
Lumbricidae	<i>Octolasion lacteum</i> *							X		X	X	
Megascolecidae	<i>Amyntas diffringens</i> *	X		X	X	X	X	X	X	X	X	
Megascolecidae	<i>Amyntas minimus</i> *			X		X		X				
Megascolecidae	<i>Amyntas rodericensis</i> *								X			
Microchaetidae	<i>Tritogenia silvicola</i>			X		X						
Microchaetidae	<i>Tritogenia turneri</i>								X			X
Microchaetidae	spp.	X	X	X								

Springtails (Class: Collembola)

Family	Genus, species	Soutpansberg						Drakensberg				
		HAN	ROD	GHP	RAT	ENT	TV	GRO	NAG	SWB	BAC	FGL
Unknown		X		X	X	X	X	X	X	X	X	

Diplurans (Class: Diplura)

Family	Genus, species	Soutpansberg						Drakensberg				
		HAN	ROD	GHP	RAT	ENT	TV	GRO	NAG	SWB	BAC	FGL
Japygidae					X				X			X

Insects (Class: Insecta)

Family	Genus, species	Soutpansberg						Drakensberg				
		HAN	ROD	GHP	RAT	ENT	TV	GRO	NAG	SWB	BAC	FGL
Acroceridae	<i>Psilodea</i> sp.		X									
Asilidae	<i>Synolcus dubius</i>									X		
Blattellidae		X	X	X		X		X	X	X	X	X
Blattidae			X				X		X	X	X	X
Bombyliidae	<i>Philoliche aethiopica</i>		X									
Braconidae						X				X		
Calliphoridae			X									
Carabidae		X	X	X	X	X	X	X	X	X	X	X
Cecidomyiidae		X										
Ceraphronidae					X		X					
Chaoboridae							X					
Chrysomelidae				X	X		X					

Millipedes (Subphylum: Myriapoda, Class: Diplopoda)

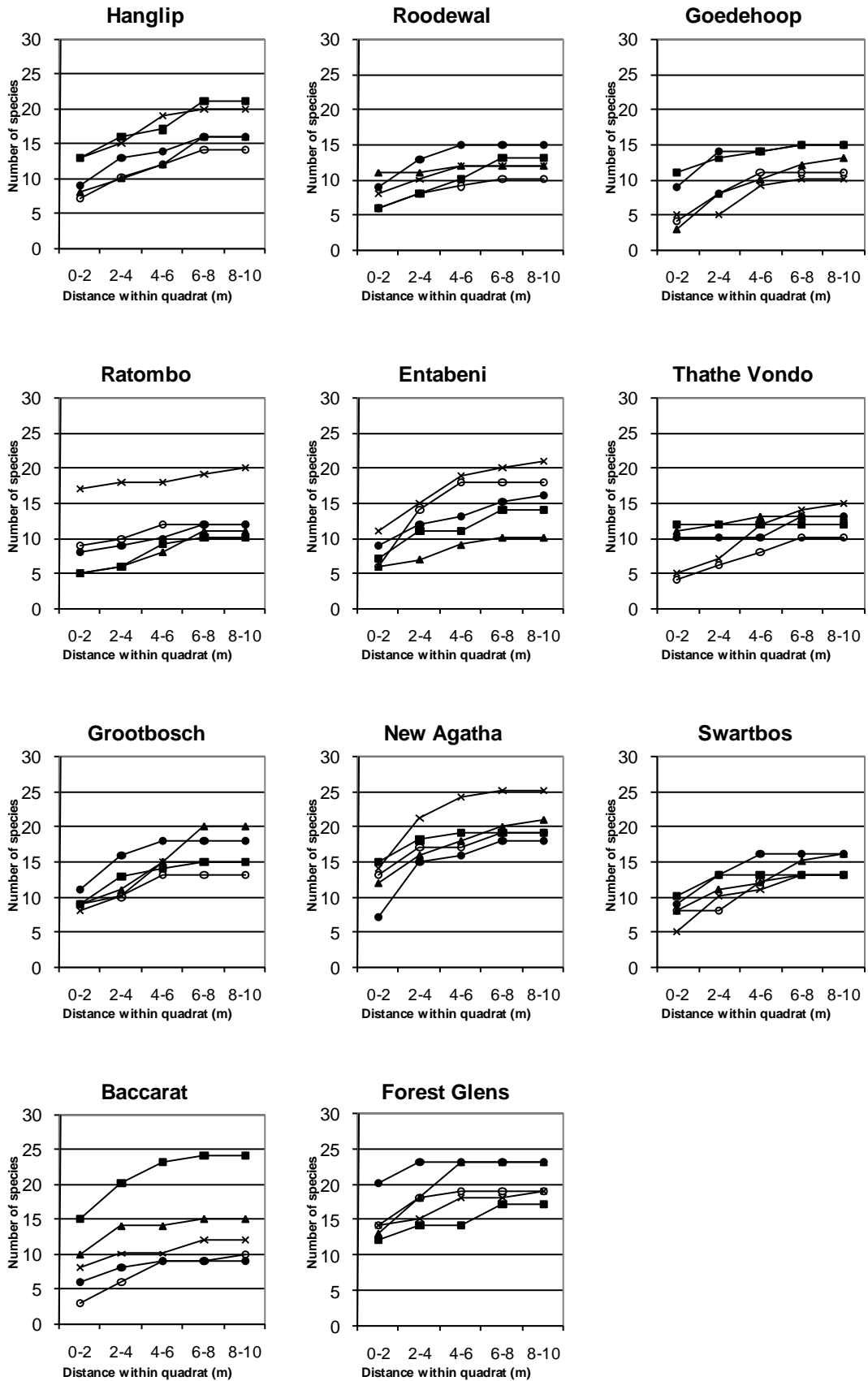
Family	Genus, species	Soutpansberg						Drakensberg				
		HAN	ROD	GHP	RAT	ENT	TV	GRO	NAG	SWB	BAC	FGL
Dalodesmidae	<i>Gnomeskelus arator</i>							X	X	X	X	X
Dalodesmidae	<i>Gnomeskelus cygniceps</i>	X		X	X	X		X	X	X	X	X
Dalodesmidae	<i>Gnomeskelus krugeri</i>		X			X						
Dalodesmidae	<i>Gnomeskelus</i> sp. n. 1						X					
Dalodesmidae	<i>Gnomeskelus</i> sp. n. 2										X	
Dalodesmidae	<i>Gnomeskelus</i> sp. n. 3							X				
Dalodesmidae	<i>Gnomeskelus</i> sp. n. 4		X									
Gomphodesmidae	<i>Ulodesmus</i> sp.		X									
Gomphodesmidae	<i>Ulodesmus propinquus</i>			X	X						X	
Odontopygidae	<i>Chaleponcus</i> sp. 1							X				
Odontopygidae	<i>Chaleponcus</i> sp. 2								X		X	
Odontopygidae	<i>Patinatius capucinus</i>	X		X	X	X	X	X	X	X	X	X
Odontopygidae	<i>Spinotarsus</i> sp. 1			X	X							
Spirostreptidae	<i>Doratogonus barbatus</i>				X							
Spirostreptidae	<i>Doratogonus herberti</i>									X	X	X
Spirostreptidae	<i>Doratogonus rugifrons</i>			X	X							
Spirostreptidae	<i>Orthoporoides</i> sp. 1								X			
Pachybolidae	<i>Centrobolus inyanganus</i>		X									
Pachybolidae	<i>Centrobolus</i> cf. <i>transvaalicus</i>			X		X	X					
Sphaerotheriidae	<i>Sphaerotherium</i> cf. <i>dicrothrix</i>	X	X									
Sphaerotheriidae	<i>Sphaerotherium dorsale</i>	X	X	X	X	X	X	X	X	X	X	X
Sphaerotheriidae	<i>Sphaerotherium hanstromi</i>		X	X	X							
Sphaerotheriidae	<i>Sphaerotherium</i> cf. <i>mahaium</i>	X	X	X		X			X		X	X
Sphaerotheriidae	<i>Sphaerotherium</i> cf. <i>perbrincki</i>	X					X	X	X	X	X	X
Sphaerotheriidae	<i>Sphaerotherium</i> sp. n. 1								X		X	

Arachnids (Class: Chelicerata, Subclass: Arachnida)

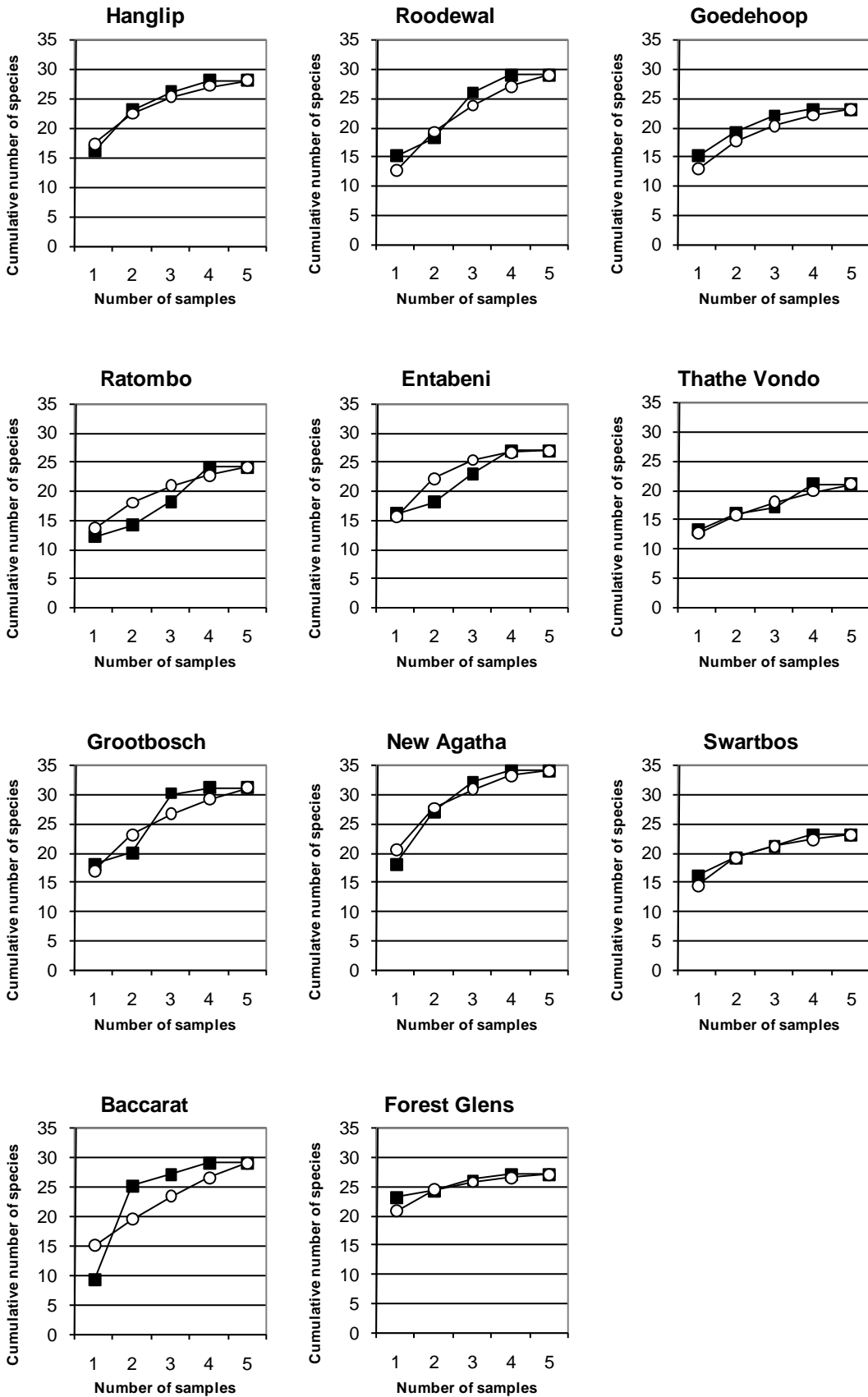
Family	Genus, species	Soutpansberg						Drakensberg				
		HAN	ROD	GHP	RAT	ENT	TV	GRO	NAG	SWB	BAC	FGL
Acari			X				X	X				X
Anapidae	<i>Crozetulus rodesiensis</i>					X						
Araneidae	<i>Araneus nigroquadratus</i>									X		
Araneidae	<i>Araneus</i> sp. 1	X		X		X	X	X				X
Araneidae	<i>Araneus</i> sp. 2									X		
Araneidae	<i>Argiope levii</i>				X							
Araneidae	<i>Caerostris sexcuspidata</i>	X		X	X	X	X	X		X	X	X
Araneidae	<i>Cyclosa insulana</i>		X		X							
Araneidae	<i>Cyphalonotus larvatus</i>		X									
Araneidae	<i>Gasteracantha milvoides</i>				X							
Araneidae	<i>Gasteracantha sanguinolenta</i>		X	X		X						
Araneidae	<i>Gasteracantha</i> sp.		X									
Araneidae	<i>Gasteracantha versicolor</i>								X			
Araneidae	<i>Gea</i> sp. 1			X	X							
Araneidae	<i>Isoxya tabulata</i>				X							
Araneidae	<i>Neoscona</i> sp.					X						
Araneidae	<i>Neoscona subfusca</i>						X			X		
Buthidae			X									
Clubionidae	<i>Clubiona</i> sp.					X						
Corinnidae	<i>Austrophaea</i> sp.						X					
Ctenidae	sp. 1								X			
Cyatholipidae	<i>Ulwembua</i> sp.	X										
Dipluridae	<i>Allothele malawi</i>								X			
Gnaphosidae	<i>Echemus</i> sp.					X						

Family	Genus, species	Soutpansberg						Drakensberg				
		HAN	ROD	GHP	RAT	ENT	TV	GRO	NAG	SWB	BAC	FGL
Gnaphosidae	<i>Setaphis</i> sp.										X	
Gnaphosidae	<i>Xerophaeus bicavus</i>			X								
Hahniidae	<i>Hahnia tabulicola</i>	X	X				X	X			X	X
Linyphiidae	<i>Meioneta</i> sp.			X								
Linyphiidae	<i>Microlinyphia sterilis</i>			X				X				X
Linyphiidae	<i>Ostearius melanopygius</i>								X			
Linyphiidae	spp.	X	X		X	X						
Linyphiidae	sp. 1									X		
Linyphiidae	sp. 2										X	
Linyphiidae	sp. 3			X								
Liocranidae	<i>Pronophaea</i> sp.			X								
Liocranidae	<i>Rhaeboctesis</i> sp.						X					
Liocranidae	sp.							X				
Lycosidae	sp. 1		X									
Lycosidae	sp. 2		X									
Lycosidae	<i>Trabae</i> sp.		X									
Mimetidae	<i>Mimetus cornutus</i>		X									X
Miturigidae	<i>Cheiramiona clavigerum</i>	X				X	X					
Miturigidae	<i>Griswoldia</i> sp.	X										
Miturigidae	<i>Syrisca</i> sp.										X	
Nemesiidae	<i>Hermacha</i> spp.	X				X						
Nemesiidae	<i>Pionothele</i> sp.											X
Nemesiidae	sp.		X									
Nesticidae	sp.							X				
Opiliones		X		X	X	X	X	X				
Orsolobidae	<i>Azanielobus lawrenzei</i>								X			
Pholcidae	<i>Smeringopus</i> sp. 1									X		
Pholcidae	<i>Smeringopus</i> sp. 2								X			
Phyxelididae	<i>Xevioso lichmadina</i>									X		
Salticidae	<i>Euophrys</i> spp.				X				X			
Salticidae	<i>Habrocestrum</i> spp.			X					X	X	X	
Salticidae	<i>Habrocestrum</i> sp. 1				X			X				
Salticidae	<i>Habrocestrum</i> sp. 2				X							
Tetragnathidae	<i>Leucauge argyrescens</i>	X		X	X	X		X		X	X	X
Tetragnathidae	<i>Leucauge decorata</i>			X		X	X	X	X	X	X	X
Tetragnathidae	<i>Leucauge levanderii</i>		X		X							
Tetragnathidae	<i>Leucauge</i> sp. 1	X	X	X	X	X	X	X		X		
Tetragnathidae	<i>Meta</i> sp. 1			X		X						
Tetragnathidae	<i>Meta</i> sp. 2							X		X	X	X
Tetragnathidae	<i>Nephila pilipes</i>		X		X							
Tetragnathidae	<i>Pachygnatha leleupi</i>	X	X		X	X	X					
Theridiidae	<i>Achaearanea</i> sp. 1							X	X	X		
Theridiidae	<i>Argyrodus</i> sp.				X							
Theridiidae	<i>Coleosoma</i> spp.	X			X		X					
Theridiidae	<i>Moneta</i> sp.				X							
Theridiidae	<i>Theridion</i> sp. 1	X				X	X	X				
Theridiidae	<i>Theridion</i> sp. 2				X							
Theridiidae	<i>Thymoites</i> sp. 1									X	X	
Theridiidae	<i>Thymoites</i> sp. 2										X	
Thomisidae	<i>Diaea punta</i>		X									
Thomisidae	<i>Misumenops rubrodecoratus</i>		X									
Thomisidae	<i>Runcinia aethiops</i>		X									
Uloboridae	<i>Hyptiotes ackermanni</i>		X									
Uloboridae	<i>Uloborus planipedius</i>				X							

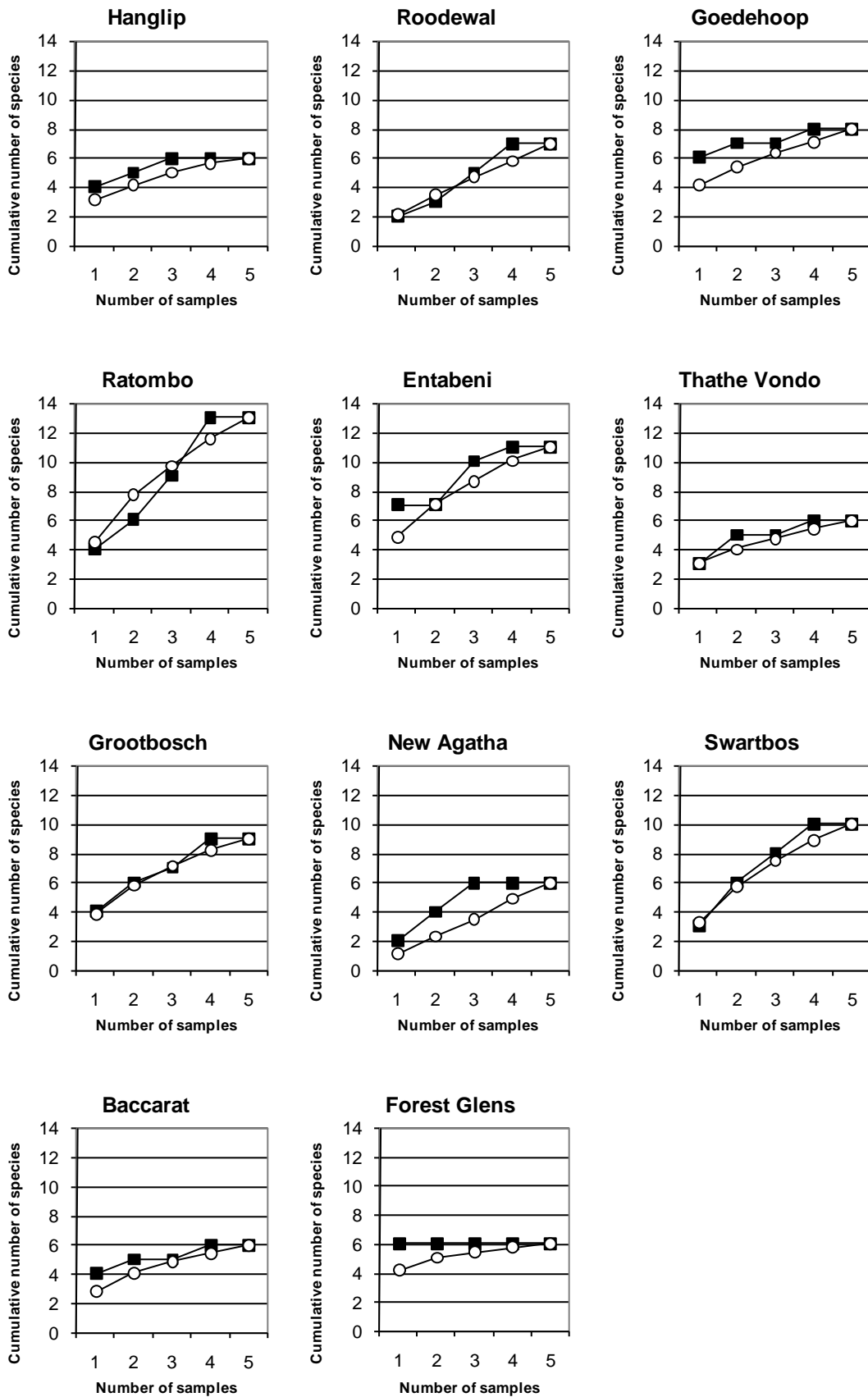
Appendix 3: Target taxa species accumulation for the five quadrats searched in each forest. Quadrats 1, 2, 3, 4 and 5 in each forest are indicated by (●, ■, ▲, x and ○) respectively.



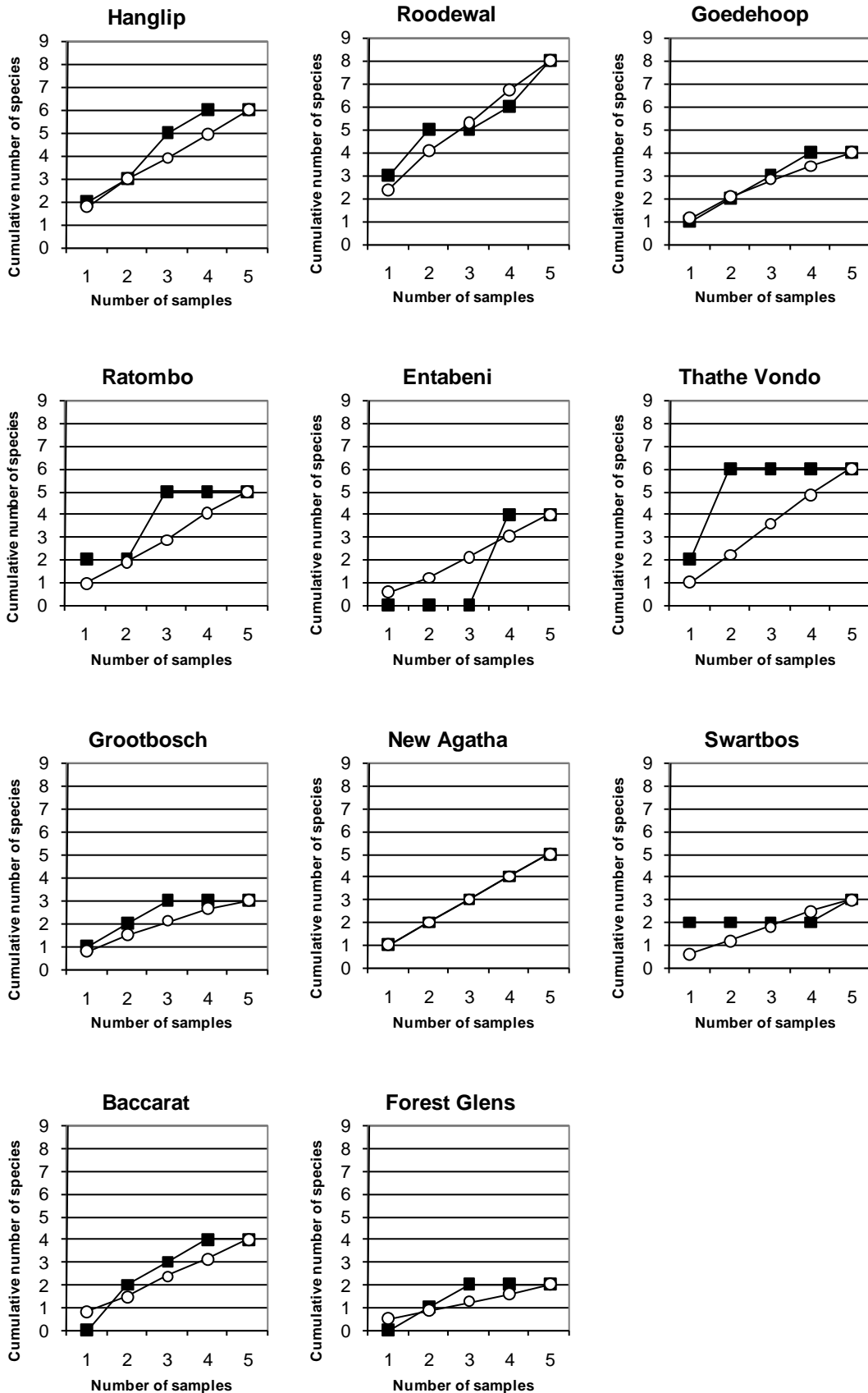
Appendix 4: Target taxa species accumulation curves for quadrats searched in each forest, where (○) is the randomized species accumulation and (■) is the field species accumulation.



Appendix 5: Web building spider species accumulation curves for transects searched in each forest, where (○) is the randomized species accumulation and (■) is the field species accumulation.



Appendix 6: Ground wandering spider species accumulation curves for pitfall traps set in each forest, where (○) is the randomized species accumulation and (■) is the field species accumulation.



Appendix 7: Values of target group richness (*S*), diversity (*NI*) and evenness (*E5*) calculated for each forest. Centipede, earthworm, web building spider, ground wandering spider and amphipod species numbers were too low to calculate evenness.

		Mean	Std. Deviation	Std. Error	95% Confidence Interval for Mean		Minimum	Maximum
					Lower Bound	Upper Bound		
Millipede richness (S)	Hanglip	3.8000	.83666	.37417	2.7611	4.8389	3.00	5.00
	Roodewal	3.6000	1.14018	.50990	2.1843	5.0157	2.00	5.00
	Goedehoop	4.4000	1.14018	.50990	2.9843	5.8157	3.00	6.00
	Ratombo	3.4000	1.67332	.74833	1.3223	5.4777	2.00	6.00
	Entabeni	3.0000	1.22474	.54772	1.4793	4.5207	2.00	5.00
	Thathe Vondo	3.0000	.00000	.00000	3.0000	3.0000	3.00	3.00
	Grootbosch	5.2000	1.30384	.58310	3.5811	6.8189	4.00	7.00
	New Agatha	6.4000	2.40832	1.07703	3.4097	9.3903	3.00	9.00
	Swartbos	3.2000	.83666	.37417	2.1611	4.2389	2.00	4.00
	Baccarat	5.0000	2.91548	1.30384	1.3800	8.6200	1.00	9.00
	Forest Glens	4.6000	.54772	.24495	3.9199	5.2801	4.00	5.00
Total	4.1455	1.70422	.22980	3.6847	4.6062	1.00	9.00	
Millipede diversity (N1)	Hanglip	2.3740	.27328	.12221	2.0347	2.7133	1.89	2.56
	Roodewal	2.2940	.88387	.39528	1.1965	3.3915	1.42	3.59
	Goedehoop	3.2680	.92091	.41184	2.1245	4.4115	2.27	4.40
	Ratombo	2.6340	1.19995	.53663	1.1441	4.1239	1.65	4.63
	Entabeni	2.0780	.90367	.40413	.9559	3.2001	1.04	3.51
	Thathe Vondo	2.2100	.47786	.21371	1.6167	2.8033	1.43	2.62
	Grootbosch	2.9900	.31289	.13993	2.6015	3.3785	2.60	3.24
	New Agatha	4.0300	.99882	.44669	2.7898	5.2702	2.65	5.43
	Swartbos	2.5540	.52605	.23526	1.9008	3.2072	2.00	3.21
	Baccarat	4.0160	1.99801	.89354	1.5351	6.4969	1.00	6.12
	Forest Glens	2.7220	.74106	.33141	1.8019	3.6421	1.86	3.89
Total	2.8336	1.08513	.14632	2.5403	3.1270	1.00	6.12	
Millipede evenness (E5)	Hanglip	.7300	.13748	.06148	.5593	.9007	.56	.94
	Roodewal	.7320	.19842	.08874	.4856	.9784	.44	.92
	Goedehoop	1.2860	1.09075	.48780	-.0683	2.6403	.64	3.23
	Ratombo	1.0560	.28272	.12644	.7050	1.4070	.66	1.37
	Entabeni	.7060	.23007	.10289	.4203	.9917	.33	.89
	Thathe Vondo	.8500	.21645	.09680	.5812	1.1188	.57	1.08
	Grootbosch	.6860	.05225	.02337	.6211	.7509	.62	.75
	New Agatha	.8760	.24255	.10847	.5748	1.1772	.65	1.28
	Swartbos	1.1240	.49054	.21938	.5149	1.7331	.87	2.00
	Baccarat	1.2475	.43912	.21956	.5488	1.9462	.89	1.88
	Forest Glens	.7640	.13202	.05904	.6001	.9279	.59	.90
Total	.9081	.43384	.05904	.7897	1.0266	.33	3.23	
Centipede richness (S)	Hanglip	2.2000	.44721	.20000	1.6447	2.7553	2.00	3.00
	Roodewal	2.2000	.83666	.37417	1.1611	3.2389	1.00	3.00
	Goedehoop	2.2000	.44721	.20000	1.6447	2.7553	2.00	3.00
	Ratombo	2.4000	1.14018	.50990	.9843	3.8157	1.00	4.00
	Entabeni	2.2000	.44721	.20000	1.6447	2.7553	2.00	3.00
	Thathe Vondo	2.0000	.00000	.00000	2.0000	2.0000	2.00	2.00
	Grootbosch	3.8000	.83666	.37417	2.7611	4.8389	3.00	5.00
	New Agatha	4.4000	.54772	.24495	3.7199	5.0801	4.00	5.00
	Swartbos	3.2000	.83666	.37417	2.1611	4.2389	2.00	4.00
	Baccarat	3.4000	.89443	.40000	2.2894	4.5106	2.00	4.00
	Forest Glens	3.2000	.83666	.37417	2.1611	4.2389	2.00	4.00
Total	2.8364	1.01404	.13673	2.5622	3.1105	1.00	5.00	
Centipede diversity (N1)	Hanglip	1.7380	.34354	.15364	1.3114	2.1646	1.16	2.00
	Roodewal	1.7980	.57924	.25904	1.0788	2.5172	1.00	2.60
	Goedehoop	1.9760	.44669	.19976	1.4214	2.5306	1.62	2.75
	Ratombo	2.0280	.83230	.37221	.9946	3.0614	1.00	3.32
	Entabeni	1.9240	.57435	.25686	1.2108	2.6372	1.33	2.83
	Thathe Vondo	1.5100	.18601	.08319	1.2790	1.7410	1.21	1.71
	Grootbosch	2.5640	.51462	.23014	1.9250	3.2030	1.90	3.27
	New Agatha	2.6480	1.01957	.45596	1.3820	3.9140	1.29	4.06
	Swartbos	2.0480	.36396	.16277	1.5961	2.4999	1.49	2.42
	Baccarat	1.8720	.42002	.18784	1.3505	2.3935	1.23	2.27
	Forest Glens	1.8880	.38571	.17249	1.4091	2.3669	1.54	2.55
Total	1.9995	.60121	.08107	1.8369	2.1620	1.00	4.06	

		Mean	Std. Deviation	Std. Error	95% Confidence Interval for Mean		Minimum	Maximum
					Lower Bound	Upper Bound		
Mollusc richness (S)	Hanglip	8.6000	2.70185	1.20830	5.2452	11.9548	6.00	12.00
	Roodewal	5.2000	2.38747	1.06771	2.2356	8.1644	2.00	8.00
	Goedehoop	4.4000	1.34164	.60000	2.7341	6.0659	2.00	5.00
	Ratombo	4.6000	1.51658	.67823	2.7169	6.4831	3.00	6.00
	Entabeni	8.6000	3.20936	1.43527	4.6151	12.5849	4.00	12.00
	Thathe Vondo	6.4000	1.51658	.67823	4.5169	8.2831	4.00	8.00
	Grootbosch	3.6000	2.07364	.92736	1.0252	6.1748	1.00	6.00
	New Agatha	6.8000	1.78885	.80000	4.5788	9.0212	4.00	8.00
	Swartbos	4.2000	1.30384	.58310	2.5811	5.8189	2.00	5.00
	Baccarat	3.0000	3.00000	1.34164	-.7250	6.7250	.00	8.00
	Forest Glens	10.6000	1.51658	.67823	8.7169	12.4831	9.00	12.00
Total	6.0000	3.02459	.40784	5.1823	6.8177	.00	12.00	
Mollusc diversity (N1)	Hanglip	5.4560	1.74261	.77932	3.2923	7.6197	4.11	8.15
	Roodewal	3.5360	.99128	.44331	2.3052	4.7668	2.00	4.59
	Goedehoop	3.9400	1.34334	.60076	2.2720	5.6080	1.65	5.00
	Ratombo	3.8780	1.00815	.45086	2.6262	5.1298	2.75	5.00
	Entabeni	6.2180	1.99237	.89101	3.7442	8.6918	3.79	8.39
	Thathe Vondo	4.3900	1.89443	.84721	2.0378	6.7422	2.92	7.58
	Grootbosch	3.2060	1.74598	.78082	1.0381	5.3739	1.00	5.11
	New Agatha	5.6540	1.53231	.68527	3.7514	7.5566	3.56	6.92
	Swartbos	3.8440	1.13641	.50822	2.4330	5.2550	1.96	4.76
	Baccarat	2.6100	2.33256	1.04315	-.2863	5.5063	.00	6.35
	Forest Glens	7.0520	1.80629	.80780	4.8092	9.2948	5.44	9.49
Total	4.5258	1.99196	.26860	3.9873	5.0643	.00	9.49	
Mollusc evenness (E5)	Hanglip	.7960	.07021	.03140	.7088	.8832	.71	.90
	Roodewal	2.0700	1.49761	.66975	.2105	3.9295	.65	4.00
	Goedehoop	1.9980	1.70264	.76144	-.1161	4.1121	1.03	5.00
	Ratombo	1.3800	.49138	.21975	.7699	1.9901	.90	2.14
	Entabeni	1.3480	1.05217	.47055	.0416	2.6544	.86	3.23
	Thathe Vondo	1.2960	1.12804	.50448	-.1046	2.6966	.49	3.27
	Grootbosch	1.5975	.50089	.25045	.8005	2.3945	1.18	2.25
	New Agatha	1.1200	.19506	.08724	.8778	1.3622	.94	1.44
	Swartbos	2.4580	1.06514	.47634	1.1355	3.7805	1.22	3.72
	Baccarat	1.8550	.76753	.38376	.6337	3.0763	1.08	2.73
	Forest Glens	.8060	.08264	.03696	.7034	.9086	.70	.90
Total	1.5126	1.00288	.13776	1.2362	1.7891	.49	5.00	
Earthworm richness (S)	Hanglip	.4000	.54772	.24495	-.2801	1.0801	.00	1.00
	Roodewal	.4000	.54772	.24495	-.2801	1.0801	.00	1.00
	Goedehoop	.4000	.89443	.40000	-.7106	1.5106	.00	2.00
	Ratombo	.2000	.44721	.20000	-.3553	.7553	.00	1.00
	Entabeni	1.0000	.00000	.00000	1.0000	1.0000	1.00	1.00
	Thathe Vondo	1.0000	.00000	.00000	1.0000	1.0000	1.00	1.00
	Grootbosch	1.2000	.44721	.20000	.6447	1.7553	1.00	2.00
	New Agatha	.8000	.44721	.20000	.2447	1.3553	.00	1.00
	Swartbos	1.4000	.89443	.40000	.2894	2.5106	.00	2.00
	Baccarat	1.0000	.00000	.00000	1.0000	1.0000	1.00	1.00
	Forest Glens	1.0000	.00000	.00000	1.0000	1.0000	1.00	1.00
Total	.8000	.59004	.07956	.6405	.9595	.00	2.00	
Earthworm diversity (N1)	Hanglip	.4000	.54772	.24495	-.2801	1.0801	.00	1.00
	Roodewal	.4000	.54772	.24495	-.2801	1.0801	.00	1.00
	Goedehoop	.3680	.82287	.36800	-.6537	1.3897	.00	1.84
	Ratombo	.2000	.44721	.20000	-.3553	.7553	.00	1.00
	Entabeni	1.0000	.00000	.00000	1.0000	1.0000	1.00	1.00
	Thathe Vondo	1.0000	.00000	.00000	1.0000	1.0000	1.00	1.00
	Grootbosch	1.0280	.06261	.02800	.9503	1.1057	1.00	1.14
	New Agatha	.8000	.44721	.20000	.2447	1.3553	.00	1.00
	Swartbos	1.0520	.66391	.29691	.2277	1.8763	.00	1.75
	Baccarat	1.0000	.00000	.00000	1.0000	1.0000	1.00	1.00
	Forest Glens	1.0000	.00000	.00000	1.0000	1.0000	1.00	1.00
Total	.7498	.51025	.06880	.6119	.8878	.00	1.84	
Web building spider richness (S)	Hanglip	3.0000	1.00000	.44721	1.7583	4.2417	2.00	4.00
	Roodewal	2.0000	1.00000	.44721	.7583	3.2417	1.00	3.00
	Goedehoop	4.0000	1.22474	.54772	2.4793	5.5207	3.00	6.00
	Ratombo	4.6000	1.81659	.81240	2.3444	6.8556	2.00	7.00
	Entabeni	4.6000	2.30217	1.02956	1.7415	7.4585	2.00	7.00
	Thathe Vondo	3.0000	.70711	.31623	2.1220	3.8780	2.00	4.00
	Grootbosch	3.8000	.83666	.37417	2.7611	4.8389	3.00	5.00
	New Agatha	1.2000	1.09545	.48990	-.1602	2.5602	.00	2.00
	Swartbos	3.4000	1.14018	.50990	1.9843	4.8157	2.00	5.00
	Baccarat	2.8000	1.09545	.48990	1.4398	4.1602	2.00	4.00
	Forest Glens	4.0000	1.22474	.54772	2.4793	5.5207	3.00	6.00
Total	3.3091	1.55006	.20901	2.8901	3.7281	.00	7.00	

		Mean	Std. Deviation	Std. Error	95% Confidence Interval for Mean		Minimum	Maximum
					Lower Bound	Upper Bound		
Web building spider diversity (N1)	Hanglip	2.6700	1.00447	.44921	1.4228	3.9172	1.65	3.78
	Roodewal	1.6940	.71682	.32057	.8040	2.5840	1.00	2.59
	Goedeheop	2.9520	.74898	.33495	2.0220	3.8820	2.28	4.16
	Ratombo	3.4160	1.81017	.80953	1.1684	5.6636	1.89	5.92
	Entabeni	3.2640	1.26666	.56647	1.6912	4.8368	1.65	4.66
	Thathe Vondo	2.4060	.60380	.27003	1.6563	3.1557	1.42	3.00
	Grootbosch	3.0680	.66807	.29877	2.2385	3.8975	2.23	3.79
	New Agatha	1.1300	1.04139	.46573	-.1631	2.4231	.00	2.00
	Swartbos	2.5660	.77080	.34471	1.6089	3.5231	1.51	3.17
	Baccarat	2.4680	1.03483	.46279	1.1831	3.7529	1.42	3.78
	Forest Glens	2.3580	.58692	.26248	1.6292	3.0868	1.64	2.92
Total	2.5447	1.10610	.14915	2.2457	2.8437	.00	5.92	
Ground wandering spider richness (S)	Hanglip	1.8000	1.09545	.48990	.4398	3.1602	.00	3.00
	Roodewal	2.4000	1.14018	.50990	.9843	3.8157	1.00	4.00
	Goedeheop	1.2000	.83666	.37417	.1611	2.2389	.00	2.00
	Ratombo	1.0000	1.41421	.63246	-.7560	2.7560	.00	3.00
	Entabeni	.8000	1.78885	.80000	-1.4212	3.0212	.00	4.00
	Thathe Vondo	1.2000	1.78885	.80000	-1.0212	3.4212	.00	4.00
	Grootbosch	.8000	.44721	.20000	.2447	1.3553	.00	1.00
	New Agatha	1.0000	.00000	.00000	1.0000	1.0000	1.00	1.00
	Swartbos	.6000	.89443	.40000	-.5106	1.7106	.00	2.00
	Baccarat	.8000	.83666	.37417	-.2389	1.8389	.00	2.00
	Forest Glens	.4000	.54772	.24495	-.2801	1.0801	.00	1.00
Total	1.0909	1.14298	.15412	.7819	1.3999	.00	4.00	
Ground wandering spider diversity (N1)	Hanglip	1.8000	1.09545	.48990	.4398	3.1602	.00	3.00
	Roodewal	2.2740	1.07006	.47855	.9453	3.6027	1.00	3.79
	Goedeheop	1.1500	.78262	.35000	.1782	2.1218	.00	2.00
	Ratombo	1.0000	1.41421	.63246	-.7560	2.7560	.00	3.00
	Entabeni	.8000	1.78885	.80000	-1.4212	3.0212	.00	4.00
	Thathe Vondo	1.1580	1.70728	.76352	-.9619	3.2779	.00	3.79
	Grootbosch	.8000	.44721	.20000	.2447	1.3553	.00	1.00
	New Agatha	1.0000	.00000	.00000	1.0000	1.0000	1.00	1.00
	Swartbos	.6000	.89443	.40000	-.5106	1.7106	.00	2.00
	Baccarat	.8000	.83666	.37417	-.2389	1.8389	.00	2.00
	Forest Glens	.4000	.54772	.24495	-.2801	1.0801	.00	1.00
Total	1.0711	1.11192	.14993	.7705	1.3717	.00	4.00	
Amphipod richness (S)	Hanglip	.8000	.44721	.20000	.2447	1.3553	.00	1.00
	Roodewal	.0000	.00000	.00000	.0000	.0000	.00	.00
	Goedeheop	1.0000	.00000	.00000	1.0000	1.0000	1.00	1.00
	Ratombo	.0000	.00000	.00000	.0000	.0000	.00	.00
	Entabeni	1.0000	.00000	.00000	1.0000	1.0000	1.00	1.00
	Thathe Vondo	.8000	.44721	.20000	.2447	1.3553	.00	1.00
	Grootbosch	.8000	.44721	.20000	.2447	1.3553	.00	1.00
	New Agatha	.8000	.44721	.20000	.2447	1.3553	.00	1.00
	Swartbos	1.0000	.00000	.00000	1.0000	1.0000	1.00	1.00
	Baccarat	1.0000	.00000	.00000	1.0000	1.0000	1.00	1.00
	Forest Glens	.6000	.54772	.24495	-.0801	1.2801	.00	1.00
Total	.7091	.45837	.06181	.5852	.8330	.00	1.00	
Amphipod diversity (N1)	Hanglip	.8000	.44721	.20000	.2447	1.3553	.00	1.00
	Roodewal	.0000	.00000	.00000	.0000	.0000	.00	.00
	Goedeheop	1.0000	.00000	.00000	1.0000	1.0000	1.00	1.00
	Ratombo	.0000	.00000	.00000	.0000	.0000	.00	.00
	Entabeni	1.0000	.00000	.00000	1.0000	1.0000	1.00	1.00
	Thathe Vondo	.8000	.44721	.20000	.2447	1.3553	.00	1.00
	Grootbosch	.8000	.44721	.20000	.2447	1.3553	.00	1.00
	New Agatha	.8000	.44721	.20000	.2447	1.3553	.00	1.00
	Swartbos	1.0000	.00000	.00000	1.0000	1.0000	1.00	1.00
	Baccarat	1.0000	.00000	.00000	1.0000	1.0000	1.00	1.00
	Forest Glens	.6000	.54772	.24495	-.0801	1.2801	.00	1.00
Total	.7091	.45837	.06181	.5852	.8330	.00	1.00	

Appendix 8: Jaccard similarity coefficients for the number of invertebrate species shared between forests. All values have been multiplied by 100 for ease of interpretation. The following abbreviations have been used for the forest names: HAN = Hanglip, ROD = Roodewal, GHP = Goedehoop, RAT = Ratombo, ENT = Entabeni, TV = Thathe Vondo, GRO = Grootbosch, NAG = New Agatha, SWB = Swartbos, BAC = Baccarat, FGL = Forest Glens. The bold lines encircle forests located in the same region. Forests sharing the mistbelt forest vegetation subtype are indicated by shading.

Site	HAN	ROD	GHP	RAT	ENT	TV	GRO	NAG	SWB	BAC	FGL
HAN	-										
ROD	21	-									
GHP	28	17	-								
RAT	22	20	29	-							
ENT	43	17	37	26	-						
TV	50	14	31	20	44	-					
GRO	30	12	30	23	39	33	-				
NAG	28	14	25	14	25	21	37	-			
SWB	24	10	27	23	26	30	43	37	-		
BAC	30	14	28	22	27	24	42	37	40	-	
FGL	38	21	27	17	26	30	42	39	33	39	-

Appendix 9: Jaccard similarity coefficients for the number of invertebrate families shared between forests. All values have been multiplied by 100 for ease of interpretation. The following abbreviations have been used for the forest names: HAN = Hanglip, ROD = Roodewal, GHP = Goedehoop, RAT = Ratombo, ENT = Entabeni, TV = Thathe Vondo, GRO = Grootbosch, NAG = New Agatha, SWB = Swartbos, BAC = Baccarat, FGL = Forest Glens. The bold lines encircle forests located in the same region. Forests sharing the mistbelt forest vegetation subtype are indicated by shading.

Site	HAN	ROD	GHP	RAT	ENT	TV	GRO	NAG	SWB	BAC	FGL
HAN	-										
ROD	50	-									
GHP	45	50	-								
RAT	41	42	52	-							
ENT	58	44	53	45	-						
TV	61	37	50	52	59	-					
GRO	59	44	59	63	57	65	-				
NAG	47	41	53	50	47	39	57	-			
SWB	52	34	41	61	50	46	68	67	-		
BAC	58	49	64	37	56	59	74	61	61	-	
FGL	64	63	48	39	57	48	57	50	45	57	-

Appendix 10: List of endemic invertebrate species sampled in Limpopo Province forests during this study. Species identified as "cf" are indicated by (*). Levels of endemism are (1) site endemics, (2) local endemics, (3) regional endemics and (4) national endemics. See Section 4.2.3 for definitions of levels.

	Level of endemism	Species	Comments
Millipedes	1	<i>Gnomeskelus</i> sp. n. 1	recorded only in Thathe Vondo
		<i>Gnomeskelus</i> sp. n. 2	recorded only in Baccarat
		<i>Gnomeskelus</i> sp. n. 3	recorded only in Grootbosch
		<i>Gnomeskelus</i> sp. n. 4	recorded only in Roodewal
	2	<i>Gnomeskelus arator</i>	
		<i>Sphaerotherium</i> sp. n.	recorded only in New Agatha and Baccarat
	3	<i>Centrobolus transvaalicus</i> *	
		<i>Doratogonus herberti</i>	
		<i>Gnomeskelus cygniceps</i>	
		<i>Patinatius capucinus</i>	
		<i>Ulodesmus propinquus</i>	
		<i>Sphaerotherium perbrinki</i> *	
	4	<i>Doratogonus barbatus</i>	
		<i>Gnomeskelus krugeri</i>	
<i>Sphaerotherium dorsale</i>			
<i>Sphaerotherium dicrothrix</i> *			
<i>Sphaerotherium hanstromi</i>			
<i>Sphaerotherium mahaium</i> *			
<i>Sphaerotherium perbrinki</i> *			
Centipedes	3	<i>Lamyctes</i> sp. n.	recorded in all forests sampled
Earthworms	1	<i>Parachilota</i> sp. n.	recorded only in Grootbosch
	2	<i>Tritogenia silvicola</i>	
		<i>Tritogenia turneri</i>	
	3	<i>Parachilota bavenda</i>	
		<i>Parachilota hutchinsoni</i>	
Molluscs	1	<i>Chlamydephorus</i> sp. n.	recorded only in Entabeni
	2	<i>Gulella harriesi</i>	
		<i>Gulella inobstructa</i>	
		<i>Gulella sibasana</i>	
		<i>Gulella</i> sp. n.	recorded in all Limpopo Province Drakensberg forests
	4	<i>Abbadia africana</i>	
		<i>Edouardia dimera</i>	
		<i>Gulella johannesburgensis</i>	
		<i>Gulella viae</i>	
		<i>Nata vernicosa</i>	
		<i>Nata viridescens</i>	
<i>Opeas florentiae</i> *			
<i>Trachycystis loveni</i> *			
<i>Trachycystis rivularis</i> *			
		<i>Trachycystis subpinguis</i> *	
Spiders	3	<i>Azaniolobus lawrenzei</i>	
	4	<i>Araneus nigroquadratus</i>	
		<i>Cheiramiona clavigera</i>	
		<i>Hyptiotes akermani</i>	
		<i>Mimetus cornutus</i>	
		<i>Xerophaeus bicavus</i>	
<i>Xevioso lichmadina</i>			
Amphipods	4	<i>Talitriator eastwoodae</i>	

Appendix 11: Millipede species recorded from selected Zimbabwean forests including the following localities: Chimanimani Mountains, Salone Forest, Chirinda Forest, Chipinge, Inyanga and Mutare (Hamer 1998). Polyxenidae, Polyzoniida and Siphonophorida were excluded from the list.

<i>Family</i>	<i>Genus, species</i>	<i>Author</i>
Gomphodesmidae	<i>Aulodesmus mossambicus</i>	(Peters, 1855)
	<i>Aulodesmus oxygonus</i>	(Peters, 1862)
	<i>Aulodesmus perarmatus</i>	Hoffman, 1966
	<i>Aulodesmus peringueyi</i>	Attems, 1928
	<i>Neodesmus mossambicus</i>	Lawrence, 1962
Odontopygidae	<i>Chaleponcus inyanga</i>	Kraus, 1960
	<i>Chaleponcus mossambiquensis</i>	Kraus, 1966
	<i>Ctenoiulus gorongozensis</i>	(Kraus, 1960)
	<i>Ctenoiulus vumbae</i>	(Kraus, 1960)
	<i>Helicochetus levifolius</i>	Attems, 1914b
	<i>Prionopetalum pulchellum</i>	Kraus, 1960
	<i>Spinotarsus lanceolatus</i>	Kraus, 1966
	<i>Spinotarsus pallicauda</i>	Kraus, 1960
	<i>Spinotarsus rhodesianus</i>	Kraus, 1960
	<i>Spinotarsus vulneratus</i>	Kraus, 1960
Pachybolidae	<i>Centrobolus immaculatus</i>	(Lawrence, 1967)
	<i>Centrobolus inyanganus</i>	(Lawrence, 1967)
	<i>Centrobolus validus</i>	(Lawrence, 1967)
	<i>Microbolus broadleyi</i>	Lawrence, 1967
Paradoxosomatidae	<i>Hoffmanina gorongozae</i>	(Lawrence, 1962)
Sphaerotheriidae	<i>Sphaerotherium kitharistes</i>	Attems, 1928
	<i>Sphaerotherium narcissei</i>	Alderweireldt, 1997
	<i>Sphaerotherium selindum</i>	Alderweireldt, 1997
Spirostreptidae	<i>Archispirostreptus conatus</i>	(Attems, 1928)
	<i>Bicoxidens flavicollis</i>	Attems, 1928
	<i>Doratogonus flavifilis</i>	(Peters, 1855)
	<i>Doratogonus subpartitus</i>	(Karsch, 1881)
	<i>Doratogonus uncinatus</i>	(Attems, 1914)
	<i>Lophostreptus carmeranii</i>	Silvestri, 1896
	<i>Orthoporoides pontifex</i>	(Attems, 1928)
	<i>Plagiotaphrus longius</i>	Attems, 1928

Appendix 12: Millipede species recorded in selected KwaZulu-Natal forests including the following localities: KZN Drakensberg forests (Giant's Castle, Cathedral Peak, Champagne Castle, Cathkin Peak, Royal Natal National Park) Karkloof and Ngeli Forest (Hamer 1998). Polyxenidae, Polyzoniida and Siphonophorida were excluded from the lists.

<i>Family</i>	<i>Genus, species</i>	<i>Author</i>
Dalodesmidae	<i>Allawrencius verrucosus</i>	Lawrence, 1962
	<i>Drakensius minor</i>	Schubart, 1956
	<i>Gnomeskelus arcuatus</i>	Verhoeff, 1939a
	<i>Gnomeskelus attemsii</i>	Verhoeff, 1939b
	<i>Gnomeskelus brincki</i>	Schubart, 1956
	<i>Gnomeskelus burius</i>	Verhoeff, 1939a
	<i>Gnomeskelus circulipes</i>	Verhoeff, 1939a
	<i>Gnomeskelus edentulus</i>	Lawrence, 1953
	<i>Gnomeskelus forcipifer</i>	Lawrence, 1953
	<i>Gnomeskelus gonoarthrodus</i>	Lawrence, 1962
	<i>Gnomeskelus laevigatus</i>	Lawrence, 1953
	<i>Gnomeskelus montivagus</i>	Verhoeff, 1939b
	<i>Gnomeskelus origensis</i>	Lawrence, 1953
	<i>Gnomeskelus processiger</i>	Lawrence, 1953
	<i>Gnomeskelus pugnifer</i>	Lawrence, 1953
	<i>Gnomeskelus serratus</i>	Verhoeff, 1939a
	<i>Gnomeskelus setosus</i>	Verhoeff, 1939b
	<i>Gnomeskelus tugelanus</i>	Verhoeff, 1939c
	<i>Platytrarpus polydesmoides</i>	Verhoeff, 1939c
	<i>Platytrarpus excelsus</i>	Lawrence, 1959
<i>Platytrarpus guduensis</i>	Schubart, 1956	
<i>Rhopaloskelus minor</i>	(Lawrence, 1958)	
Gomphodesmidae	<i>Ulodesmus natalensis</i>	Lawrence, 1953
	<i>Ulodesmus simplex</i>	Lawrence, 1953
Odontopygidae	<i>Patinatius bidentatus</i>	Kraus, 1960
	<i>Spinotarsus avirostris</i>	Kraus, 1960
	<i>Spinotarsus debilis</i>	(Attems, 1928)
	<i>Spinotarsus hospitii</i>	Kraus, 1960
	<i>Spinotarsus triangulosus</i>	Kraus, 1960
Pachybolidae	<i>Centrobolus rubricollis</i>	(Schubart, 1966)
	<i>Centrobolus tricolor</i>	(Lawrence, 1967)
Sphaerotheriidae	<i>Sphaerotherium dorsale</i>	(Gervais, 1847)
	<i>Sphaerotherium dorsaloide</i>	Silvestri, 1910
	<i>Sphaerotherium mahaium</i>	Schubart, 1958a
	<i>Sphaerotherium perbrincki</i>	Schubart, 1958a
	<i>Sphaerotherium rotundatum</i>	Brandt, 1833
<i>Sphaerotherium tomentosum</i>	Schubart, 1958a	
Spirostreptidae	<i>Doratogonus cristulatus</i>	(Porat, 1872)
	<i>Doratogonus subpartitus</i>	(Karsch, 1881)
	<i>Orthoporoides pyrhocephalus</i>	(L. Kock, 1865)
Vaalogonopodidae	<i>Phygoxerotes myrmecophilus</i>	Lawrence, 1953

Appendix 13: Terrestrial mollusc species recorded from selected Zimbabwean forests, including the following localities: Vumba Mountains, Chirinda Forest and Inyanga (Natal Museum Mollusc Database, van Bruggen 1971; 1980; A.C. van Bruggen 2003, pers. comm.).

<i>Family</i>	<i>Genus, species</i>	<i>Author</i>
Achatinidae	<i>Achatina immaculata</i>	Lamarck, 1822
	<i>Achatina sandgroundi</i>	(Bequaert, 1950)
	<i>Laevicaulis alte</i>	(Ferussac, 1821)
	<i>Laevicaulis natalensis</i>	(Krauss, 1848)
	<i>Pseudoglessula cressyi</i>	Connolly, 1925
Cerastidae	<i>Edouardia metuloides</i>	(Smith, 1899)
Charopidae	<i>Trachycystis bernardinae</i>	Connolly, 1925
	<i>Trachycystis sylvicola</i>	van Bruggen & Verdcourt, 1965
Chlamydephoridae	<i>Chlamydephorus septentrionalis</i>	Forcart, 1967
Euconulidae	<i>Afroconulus diaphanus</i>	(Connolly, 1922)
Pomatiasidae	<i>Chondrocyclus chirindae</i>	van Bruggen, 1986
	<i>Tropidophora insularis</i>	(Pfeiffer, 1852)
	<i>Tropidophora nyasana</i>	(Smith, 1899)
Streptaxidae	<i>Afristeptaxis elongatus</i>	(Fulton, 1899)
	<i>Gulella ceciliae</i>	van Bruggen, 1971
	<i>Gulella farquhari</i>	(Melvill & Ponsonby, 1895)
	<i>Gulella lawrencei</i>	van Bruggen, 1964
	<i>Gulella vicina</i>	(Smith, 1899)
	<i>Streptostele herma</i>	Connolly, 1912
Subulinidae	<i>Streptostele incospicua</i>	van Bruggen, 1964
	<i>Curvella nyasana</i>	Smith, 1899
	<i>Pseudopeas victoriae</i>	Connolly, 1919
Urocyclidae	<i>Atoxonoides bruggeni</i>	(Forcart, 1967)
	<i>Atoxonoides meridionalis</i>	Forcart, 1967
	<i>Dendrolimax osborni</i>	Pilsbry, 1919
	<i>Elisolimax flavescens</i>	(Keferstein, 1866)
	<i>Leptichnoides verdcourti</i>	(Forcart, 197)
	<i>Thapsia insimulans</i>	Smith, 1899
	<i>Thapsia pinguis</i>	(Krauss, 1848)
	<i>Trochonanina consociata</i>	(Smith, 1899)
Veronicellidae	<i>Urocyclus kirki</i>	Gray, 1864
	<i>Gymnarion chirindicus</i>	Binder, 1981
	<i>Zingis chirindensis</i>	van Bruggen & Verdcourt, 1968
Vertiginidae	<i>Zingis morrumbalensis</i>	(Melvill & Ponsonby, 1894)
	<i>Nesopupa vengoensis</i>	Connolly, 1925

Appendix 14: Mollusc species recorded in Karkloof forest, KwaZulu-Natal
(Natal Museum Mollusc Database).

<i>Family</i>	<i>Genus, species</i>	<i>Author</i>
Acatinidae	<i>Achatina granulata</i>	(Krauss, 1848)
Cerastidae	<i>Edouardia dimera</i>	(Melville & Ponsonby, 1901)
Charopidae	<i>Trachycystis conisalea</i>	(Melville & Ponsonby, 1892)
	<i>Trachycystis glanvilliana</i>	(Ancey, 1893)
	<i>Trachycystis inclara</i>	(Morelet, 1889)
	<i>Trachycystis loveni</i>	(Krauss, 1848)
	<i>Trachycystis rudicostata</i>	Connolly, 1922
	<i>Trachycystis subpinguis</i>	Connolly, 1922
Clausiliidae	<i>Abbadia africana</i>	(Melville & Ponsonby, 1899)
Cyclophoridae	<i>Chondrocyclus isipingoensis</i>	(Sturany, 1898)
Euconulidae	<i>Afroconulus diaphanus</i>	(Connolly, 1922)
Helicarionidae	<i>Kaliella barrakporensis</i>	(Pfeiffer, 1852)
	<i>Kaliella euconuloides</i>	Melville & Ponsonby, 1908
Hydrocenidae	<i>Hydrocena noticola</i>	Benson, 1856
Orculidae	<i>Fauxulus mcbeanianus</i>	Melville & Ponsonby, 1901
Pomatiasidae	<i>Tropidophora insularis</i>	(Pfeiffer, 1852)
Punctidae	<i>Paralaoma hottentota</i>	(Melville & Ponsonby, 1891)
Pupillidae	<i>Lauria dadion</i>	(Benson, 1864)
	<i>Pupilla fontana</i>	(Krauss, 1848)
Rhytididae	<i>Nata vernicosa</i>	(Krauss, 1848)
	<i>Nata viridescens</i>	(Melville & Ponsonby, 1891)
	<i>Natalina cafra</i>	(Ferussac, 1821)
Streptaxidae	<i>Gulella columella</i>	(Melville & Ponsonby, 1901)
	<i>Gulella darglensis</i>	(Melville & Ponsonby, 1908)
	<i>Gulella delicatula</i>	(Pfeiffer, 1856)
	<i>Gulella farquhari</i>	(Melville & Ponsonby, 1895)
	<i>Gulella formosa</i>	(Melville & Ponsonby, 1898)
	<i>Gulella isipingoensis</i>	(Sturany, 1898)
	<i>Gulella maritzburgensis</i>	(Melville & Ponsonby, 1893)
	<i>Gulella obovata</i>	(Pfeiffer, 1855)
Subulinidae	<i>Euonyma lymnaeiformis</i>	(Melville & Ponsonby, 1901)
	<i>Euonyma natalensis</i>	(Burnup, 1905)
	<i>Opeas florentiae</i>	(Melville & Ponsonby, 1901)
	<i>Opeas strigile</i>	(Melville & Ponsonby, 1901)
Succineidae	<i>Succinea striata</i>	Krauss, 1848
Vertiginidae	<i>Pupisoma harpula</i>	(Reinhardt, 1886)
	<i>Pupisoma orcula</i>	(Benson, 1856)