

**RESPONSE OF CARABID AND CICINDELID
BEETLES TO VARIOUS TYPES OF LANDSCAPE
DISTURBANCES**

By

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Insects, in view of their small size, high chitin content, great population variability and harvesting difficulties, generally are not particularly valuable as a direct resource for humans. Their value lies in the role they play in ecosystem processes. The landscape in which they occur must be conserved and utilized sustainably. Insects should be preserved per se, so that their activities can maintain ecosystems and also benefit man. Besides, insects, as with other biota, are our earthly companions. Without them we would indeed suffer from a great loneliness of spirit.

M. J. Samways (1994)

PREFACE

This study was carried out in the Department of Zoology and Entomology, University of Natal, Pietermaritzburg, from February, 1994 to March 1998, under the supervision of Professor Michael J. Samways. This is the author's original work and has not been submitted in any other form to another university. Where use was made of the work of others, it has been duly acknowledged in the text

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ABSTRACT

A study of carabids and cicindelids was carried out in eastern South Africa using the same methodology as has been used in the northern hemisphere to obtain a southern hemisphere perspective. The study used the macroecology approach to compare patterns and responses of these animals to anthropogenic disturbances in visually similar habitats (forests, grasslands). Although this is essentially a local component of a larger macroecological study, it is shown that even though species and identities differ between the north and southern hemispheres, the general patterns of community response to anthropogenic disturbances are surprisingly similar.

Changes in carabid assemblages were assessed across eight sites or landscape elements experiencing a range of disturbance types, both regular and irregular (such as mowing, fire, irrigation, fertilizers, pesticides, forestry). Direct comparisons were made with similar studies in the Palaearctic. Species diversity, seasonal population variations, population phenology, spatial patterns and mean body size of species assemblages relative to the landscape elements are described. As in the north, intensively disturbed biotopes were impoverished, and natural patches of moist forest acted as habitat sources for these disturbed sinks. Roadside verges were species-rich analogues of natural habitats. The mean body size of carabid assemblages in forest and grassland sites decreased with increasing intensity of disturbance. One contrary comparison with the north was that a plantation, in this case macadamia, was exceptionally rich in carabid species and individuals.

Classification and ordination methods identified and characterised the eight sites to six ecological meaningful biotopes for carabids and cicindelids. This also allowed inferences as to how the various landscape disturbances in natural forests, planted pine forests, macadamia plantation, recreational park, road verge grasslands and hayfields affect carabid and cicindelid species richness and abundance. Species assemblages that responded to these anthropogenic impacts were potential indicator groups that can assist in the planning and management of forest and grassland landscapes for conservation of biodiversity. Some management recommendations for these landscapes are given.

Individual species-environment relations were investigated using both univariate and multivariate analyses. The solutions to these analyses were then used to describe how species

are distributed along major environmental gradients. It was shown that soil characteristics (pH, moisture, twig and/or leaf litter) determine carabid and cicindelid assemblages. Land-use and management regimes influence these patterns. The effect of altitude is masked by the presence of soil characteristics in a multivariate analysis, and more so in the presence of pH and moist soil-sand gradients with changing altitude. In the absence of soil characteristics and in univariate analysis, altitude becomes very important. Altitude has therefore an indirect effect in that it determines climate, which, in turn, determines soil and vegetation type which then determines species presence and abundance.

It is concluded that the macroecological approach has great potential for teasing apart local effects from global ones, and can contribute to the conservation of biodiversity at both small and large scales.

LIST OF CONTENTS

PREFACE	i
ACKNOWLEDGEMENTS	ii
ABSTRACT	iii
LIST OF TABLES	xvi
LIST OF FIGURES	xxvi

CHAPTER 1

INTRODUCTION

.	1
1.1 THE MACROECOLOGICAL APPROACH	1
1.2 LANDSCAPE DISTURBANCES FACTORS AND BIOINDICATORS	2
1.2.1 Bioindicators	3
1.2.2 Intermediate disturbance hypothesis	4
1.2.3 Burning	4

1.2.4	Road verges and prescribed autumn burning disturbance	7
1.2.5	Mowing	9
1.2.6	Woodlands and forests	9
1.2.7	Agriculture	10
1.2.8	Seasonal variations	11
1.3	CONSERVATION STRATEGIES FOR INVERTEBRATES	12
1.4	GROUND BEETLES AS SUBJECTS	12
1.4.1	Landscape disturbances and body size distribution of carabid beetles	14
1.5	AIMS OF THIS STUDY	14

CHAPTER 2

SITES

.	17
2.1	INTRODUCTION	17
2.2	FERNCLIFFE NATURE RESERVE	22
2.2.1	Situation and topography	22
2.2.2	History	22
2.2.3	Geology	22

2.2.4	Climate	23
2.2.5	Hydrology	23
2.2.6	Vegetation	24
2.2.7	Fauna	25
2.3	BISLEY NATURE RESERVE	26
2.3.1	Situation and Topography	26
2.3.2	History	26
2.3.3	Geology	26
2.3.4	Climate	26
2.3.5	Hydrology	26
2.3.6	Vegetation	27
2.3.7	Fauna	28
2.4	UKULINGA RESEARCH FARM	28
2.4.1	Situation and Topography	28
2.4.2	Vegetation	28

CHAPTER 3

MATERIALS AND METHODS

.	34
-----------	----

3.1	INTRODUCTION	34
3.2	MATERIALS	35
	3.2.1 Pitfall traps	35
	3.2.2 Pitfall trap modifications	35
	3.2.3 Pitfall trap installation	37
	3.2.4 Pitfall trap roofing	38
	3.2.5 Collecting fluid	38
	3.2.6 Collecting the trap catch	39
3.3	METHODS	40
	3.3.1 Pitfall trap sampling	40
	3.3.2 Window trap sampling	40
	3.3.2.1 Glass window traps	40
	3.3.2.2 PVC-netting material window trap	42
	3.3.3 Visual sampling	42
	3.3.4 Environmental variables	43
	3.3.5 Mean body sizes	48
3.4	DATA ANALYSIS	48
	3.4.1 Introduction	48
	3.4.2 Univariate methods	49
	3.4.3 Multivariate methods	51
3.5	BEETLE IDENTIFICATION	55

CHAPTER 4

RESULTS

.	56
4.1 SAMPLING METHODS	56
4.1.1 Numbers of species and individuals caught	56
4.1.2 Window trapping	56
<i>4.1.2.1 Glass window traps</i>	<i>56</i>
<i>4.1.2.2 PVC-netting material window trap</i>	<i>58</i>
4.1.3 Visual searching	58
4.1.4 Pitfall trapping	60
4.2 SPECIES CUMULATIVE CURVES	61
4.2.1 Species cumulative curve over two annual sampling seasons	61
4.2.2 Species cumulative curves for each annual sampling season	61
4.2.3 Species cumulative curves at each of the eight sites	61
4.3 SEASONAL POPULATION VARIATION	64
4.3.1 Seasonal population variation at all sites	64
4.3.2 Comparison of seasonal population variation between forests and grasslands at the same altitude	68

4.3.3	Comparison of seasonal population variation between primary and secondary forests and grasslands	73
4.3.4	Seasonal population variation as number of species	76
4.3.5	Proportionate numbers of carabids and cicindelids over time.	80
4.3.6	Population phenology in eight sites: multivariate analysis (PCA) of species abundance over time	81
4.4	PATTERNS OF DIVERSITY AND ABUNDANCE AMONG SITES	94
4.4.1	General abundance	94
4.4.2	General species richness	96
4.4.3	Comparison of spatial population patterns between forests and grasslands at the same altitude	97
4.4.4	Comparison of spatial population patterns between primary and secondary forests and grasslands	98
4.4.5	Proportionate numbers of carabids and cicindelid in the eight sites	100
4.5	SPECIES DIVERSITY	101
4.5.1	Shannon's diversity H' of all eight sites	101
4.5.2	Species richness Margalef's R_1 , Shannon's diversity H' and Pielou's evenness J' in the eight sites.	108

4.5.3	Diversity measures in point habitats at each of the eight sites . . .	109
4.5.4	Proportion of carabids and cicindelid species in point habitats of the eight sites.	110
4.5.5	Rarefaction model for species richness	110
4.5.6	The lognormal distribution model	111
4.5.7	Comparison of three species richness indices: Margalef's index (R1), rarefaction model and the theoretical number of species (S*)	115
4.5.8	Caswell's neutral model used to estimate environmental stress levels	116
4.6	GRAPHICAL/DISTRIBUTIONAL MODELS FOR DETECTING EFFECTS OF ENVIRONMENTAL STRESS.	120
4.6.1	x ² geometric plots	120
4.6.2	Rank abundance (dominance) curves	125
4.7	MULTIVARIATE ANALYSIS OF SPECIES DATA	127
4.7.1	Community classification and ordination using PRIMER. . .	127
4.7.1.1	<i>Classification and MDS ordination at the landscape level</i>	<i>127</i>
4.7.1.2	<i>Classification and MDS ordination at the point habitat level</i>	

.	131
4.7.1.3 Linking community structure to environmental variables	
.	135
4.7.2 Ordination of species using CANOCO.	147
4.7.2.1 Ordination (CA and CCA) at the landscape level.	147
4.7.2.2 Ordination (CA) at the point habitat level.	167
4.8 DIFFERENCES IN THE APPLICATION OF CANOCO AND PRIMER.	178
4.9 MEAN BODY SIZE OF SPECIES ASSEMBLAGES.	180
4.10 TAXONOMIC SUMMARY OF SPECIES.	182

CHAPTER 5

DISCUSSION

.	185
5.1 SAMPLING METHODS.	185
5.1.1 Number of species and individuals sampled.	185
5.1.2 Collecting methods.	187
5.1.2.1 Pitfall trapping.	187
5.1.2.2 Glass window traps.	188
5.1.2.3 PVC-netting window traps.	188

5.1.2.4	<i>Visual searching</i>	189
5.1.2.5	<i>Linking collecting methods to data analyses</i>	192
5.1.3	Collecting preservative	193
5.2	SPECIES CUMULATIVE CURVES	194
5.3	SEASONAL POPULATION VARIATION	195
5.3.1	Effect of altitude	195
5.3.2	Activity patterns	196
5.3.3	Effect of disturbance	197
5.3.4	Population phenology: multivariate analysis (PCA) of species abundances over time	200
5.4	SPECIES DIVERSITY AND THE INTERMEDIATE DISTURBANCE HYPOTHESIS	201
5.4.1	Potential problems of diversity indices	202
5.4.2	Caswell's neutral model and estimating environmental stress levels	207
5.5	EFFECT OF DISTURBANCE ON BODY SIZE	208
5.6	GRAPHICAL DISTRIBUTION PATTERNS: SPECIES-ABUNDANCE RELATIONSHIPS	209
5.6.1	x² geometric plots	210
5.6.2	Lognormal distribution model	212
5.7	SPECIES - ENVIRONMENT RELATIONSHIPS	214
5.7.1	Ordination at the landscape level	214

5.7.1.1	<i>Effect of soil characteristics</i>	214
5.7.1.2	<i>Effect of land-use\ management</i>	216
5.7.1.3	<i>Effect of habitat type</i>	218
5.7.2	Ordination of point habitats	221
5.8	IMPORTANCE OF USING TWO ORDINATION METHODS.	222
5.9	SIGNIFICANCE OF FINDINGS IN A MACROECOLOGICAL CONTEXT	
	<i>.</i>	223

CHAPTER 6

RECOMMENDATIONS FOR CARABID AND BIODIVERSITY CONSERVATION MANAGEMENT

	<i>.</i>	231
6.1	AIMS OF MANAGEMENT.	231
6.2	IMPLICATIONS FOR CONSERVATION MANAGEMENT.	232
6.2.1	Forests and woodlands	232
6.2.2	Recreational parks	237
6.2.3	Road verge grasslands	237
6.2.4	Agriculture: macadamia plantation	241
6.3	THE NEED FOR INTEGRATED MANAGEMENT.	243

CHAPTER 7

CONCLUSIONS

. 245

REFERENCES 250

APPENDIX 1 TABLES IN CHAPTER 3 282

APPENDIX 2 TABLES IN CHAPTER 4 285

**APPENDIX 3 PHOTOGRAPHS OF SOME OF THE
LARGER CARABIDS AND
CICINDELIDS COLLECTED. . . 307**

LIST OF TABLES

Table 2.1:	A summary of the eight landscape elements (sites) used in this study, with their abbreviations pertaining to type of disturbance or landuse. Four point habitats per landscape element were sampled. Further details can be found in the text, (Chapter 3, Section 3.3.4). Metres above sea level (m.a.s.l.). 21
Table 3.1:	Environmental data arranged for the 32 point habitats in the whole study area. Each of the eight sites (S1 to S8) has four point habitats, e.g. S1 (1, 2, 3, 4). The scores of the environmental variables in column one, are explained in the text, Section 3.3.4. Escarpment (E); Savannah (S); Primary Forest (PF); Secondary Forest (SF); Secondary Grassland (SG); Primary Grassland (PG); Nature Management (NM); <i>Pine</i> Plantation (PP); Park (PA); Road Verge (RV); <i>Macadamia</i> Plantation (MP); Grassland Field (FD); Clay Loam (CL); Sandy Loam (SL); Loam (L); Silty Clay (SIC); Silty Clay Loam (SCL); Clay (C); Fine Sand (FS); Medium Sand (MS); Coarse Sand (CS). 44
Table 3.2:	Environmental data as mean values of the four point habitats per site (Table 3.1) arranged for each of the eight sites (1 - 8). The scores are explained in the text (Section 3.3.4). 45
Table 3.3:	Climate data for Savanna Zone over the study period. (a) totals and averages for maximum temperature (°C), (b) totals and averages for rain (mm), (c) totals and averages for maximum humidity (%). . . . 283
Table 3.4:	Climate data for Escarpment Zone over the study period. (a) totals and averages for maximum temperature (°C), (b) totals and averages for rain (mm), (c) totals and averages for maximum humidity (%). . . . 284
Table 4.1:	Species list of Carabidae and Cicindelidae collected over the whole study

period. Undescribed species (*). Illustrations of some of these species can be seen in Appendix 3 57

Table 4.1.1: Spearman correlation coefficients (calculated with SPSS 6.1) between climate and species in change in species abundance and richness over monthly samples ($n=12$), for two annual sampling seasons and as a sum of both seasons, in forest and grassland sites within the Savanna Zone. Significance at the $P=0.05$ level is shown by (*) and Significance at the $P=0.01$ level is shown by (**). 66

Table 4.1.2: Spearman correlation coefficients (calculated with SPSS 6.1) between climate and species in change in species abundance and richness over monthly samples ($n=12$), for two annual sampling seasons and as a sum of both seasons, in forest and grassland sites within the Escarpment Zone. Significance at the $P=0.05$ level is shown by (*) and Significance at the $P=0.01$ level is shown by (**). 66

Table 4.2: Number of individuals of carabid and cicindelid species as code numbers (see Table 4.1 for actual names) and cumulative number of species (Cum. No.), recorded for each monthly replicate over the first sampling season (June 1994 - May 1995), arranged for each of the four point habitats (1 2 3 4) at Site 1. Blank cells indicate no species were recorded in the four point habitats. Total abundance (Tot. Abu.); Total number of species (Tot. No. Sp.). 286

Table 4.3: Number of individuals of carabid and cicindelid species as code numbers (see Table 4.1 for actual names) and cumulative number of species (Cum. No.), recorded for each monthly replicate over the first sampling season (June 1994 - May 1995), arranged for each of the four point habitats (5 6 7 8) at Site 2. Blank cells indicate no species were recorded in the four point habitats. Total abundance (Tot. Abu.); Total number of species (Tot. No. Sp.). 286

Table 4.4: Number of individuals of carabid and cicindelid species as code numbers

(see Table 4.1 for actual names) and cumulative number of species (Cum. No.), recorded for each monthly replicate over the first sampling season (June 1994 - May 1995), arranged for each of the four point habitats (9 10 11 12) at Site 3. Blank cells indicate no species were recorded in the four point habitats. Total abundance (Tot. Abu.); Total number of species (Tot. No. Sp.). 287

Table 4.5: Number of individuals of carabid and cicindelid species as code numbers (see Table 4.1 for actual names) and cumulative number of species (Cum. No.), recorded for each monthly replicate over the first sampling season (June 1994 - May 1995), arranged for each of the four point habitats (13 14 15 16) at Site 4. Blank cells indicate no species were recorded in the four point habitats. Total abundance (Tot. Abu.); Total number of species (Tot. No. Sp.). 287

Table 4.6: Number of individuals of carabid and cicindelid species as code numbers (see Table 4.1 for actual names) and cumulative number of species (Cum. No.), recorded for each monthly replicate over the first sampling season (June 1994 - May 1995), arranged for each of the four point habitats (17 18 19 20) at Site 5. Blank cells indicate no species were recorded in the four point habitats. Total abundance (Tot. Abu.); Total number of species (Tot. No. Sp.). 288

Table 4.7: Number of individuals of carabid and cicindelid species as code numbers (see Table 4.1 for actual names) and cumulative number of species (Cum. No.), recorded for each monthly replicate over the first sampling season (June 1994 - May 1995), arranged for each of the four point habitats (21 22 23 24) at Site 6. Blank cells indicate no species were recorded in the four point habitats. Total abundance (Tot. Abu.); Total number of species (Tot. No. Sp.). 288

Table 4.8: Number of individuals of carabid and cicindelid species as code numbers (see Table 4.1 for actual names) and cumulative number of species (Cum.

No.), recorded for each monthly replicate over the first sampling season (June 1994 - May 1995), arranged for each of the four point habitats (25 26 27 28) at Site 7. Blank cells indicate no species were recorded in the four point habitats. Total abundance (Tot. Abu.); Total number of species (Tot. No. Sp.). 289

Table 4.9: Number of individuals of carabid and cicindelid species as code numbers (see Table 4.1 for actual names) and cumulative number of species (Cum. No.), recorded for each monthly replicate over the first sampling season (June 1994 - May 1995), arranged for each of the four point habitats (29 30 31 32) at Site 8. Blank cells indicate no species were recorded in the four point habitats. Total abundance (Tot. Abu.); Total number of species (Tot. No. Sp.). 289

Table 4.10: Number of individuals of carabid and cicindelid species as code numbers (see Table 4.1 for actual names) and cumulative number of species (Cu. No.), recorded over the first sampling season (June 1994 - May 1995), for the whole sampling area, and arranged for each of the 12 monthly replicates. Total abundance (Tot. Abu.); Total number of species (Tot. No. Sp.). 290

Table 4.11: Number of individuals of carabid and cicindelid species as code numbers (see Table 4.1 for actual names) and cumulative number of species (Cum. No.), recorded for each monthly replicate over the second sampling season (June 1995 - May 1996), arranged for each of the four point habitats (1 2 3 4) at Site 1. Blank cells indicate no species were recorded in the four point habitats. Total abundance (Tot. Abu.); Total number of species (Tot. No. Sp.). 292

Table 4.12: Number of individuals of carabid and cicindelid species as code numbers (see Table 4.1 for actual names) and cumulative number of species (Cum. No.), recorded for each monthly replicate over the second sampling season (June 1995 - May 1996), arranged for each of the four point

habitats (5 6 7 8) at Site 2. Blank cells indicate no species were recorded in the four point habitats. Total abundance (Tot. Abu.); Total number of species (Tot. No. Sp.). 292

Table 4.13: Number of individuals of carabid and cicindelid species as code numbers (see Table 4.1 for actual names) and cumulative number of species (Cum. No.), recorded for each monthly replicate over the second sampling season (June 1995 - May 1996), arranged for each of the four point habitats (9 10 11 12) at Site 3. Blank cells indicate no species were recorded in the four point habitats. Total abundance (Tot. Abu.); Total number of species (Tot. No. Sp.). 293

Table 4.14: Number of individuals of carabid and cicindelid species as code numbers (see Table 4.1 for actual names) and cumulative number of species (Cum. No.), recorded for each monthly replicate over the second sampling season (June 1995 - May 1996), arranged for each of the four point habitats (13 14 15 16) at Site 4. Blank cells indicate no species were recorded in the four point habitats. Total abundance (Tot. Abu.); Total number of species (Tot. No. Sp.). 293

Table 4.15: Number of individuals of carabid and cicindelid species as code numbers (see Table 4.1 for actual names) and cumulative number of species (Cum. No.), recorded for each monthly replicate over the second sampling season (June 1995 - May 1996), arranged for each of the four point habitats (17 18 19 20) at Site 5. Blank cells indicate no species were recorded in the four point habitats. Total abundance (Tot. Abu.); Total number of species (Tot. No. Sp.). 294

Table 4.16: Number of individuals of carabid and cicindelid species as code numbers (see Table 4.1 for actual names) and cumulative number of species (Cum. No.), recorded for each monthly replicate over the second sampling season (June 1995 - May 1996), arranged for each of the four point habitats (21 22 23 24) at Site 6. Blank cells indicate no species were

recorded in the four point habitats. Total abundance (Tot. Abu.); Total number of species (Tot. No. Sp.). 294

Table 4.17: Number of individuals of carabid and cicindelid species as code numbers (see Table 4.1 for actual names) and cumulative number of species (Cum. No.), recorded for each monthly replicate over the second sampling season (June 1995 - May 1996), arranged for each of the four point habitats (25 26 27 28) at Site 7. Blank cells indicate no species were recorded in the four point habitats. Total abundance (Tot. Abu.); Total number of species (Tot. No. Sp.). 295

Table 4.18: Number of individuals of carabid and cicindelid species as code numbers (see Table 4.1 for actual names) and cumulative number of species (Cum. No.), recorded for each monthly replicate over the second sampling season (June 1995 - May 1996), arranged for each of the four point habitats (29 30 31 32) at Site 8. Blank cells indicate no species were recorded in the four point habitats. Total abundance (Tot. Abu.); Total number of species (Tot. No. Sp.). 295

Table 4.19: Number of individuals of carabid and cicindelid species as code numbers (see Table 4.1 for actual names) and cumulative number of species (Cu. No.), recorded over the second sampling season (June 1995 - May 1996), for the whole sampling area, and arranged for each of the 12 monthly replicates. Total abundance (Tot. Abu.); Total number of species (Tot. No. Sp.). 296

Table 4.20: Sum of the number of individuals of carabid and cicindelid species as code numbers (see Table 4.1 for actual names) and cumulative number of species (Cu. No.), recorded over the two sampling seasons (June 1994 - May 1996), for the whole sampling area, and arranged for each of the 12 monthly replicates. Total abundance (Tot. Abu.); Total number of species (Tot. No. Sp.).
. 297

Table 4.21:	Number of individuals of carabid and cicindelid species as code numbers (see Table 4.1 for actual names) recorded over the first sampling season (June 1994 - May 1995), for the whole sampling area, arranged for each of the eight landscape elements (Sites 1-8).	298
Table 4.22:	Number of individuals of carabid and cicindelid species as code numbers (see Table 4.1 for actual names) recorded over the second sampling season (June 1995 - May 1996), for the whole sampling area, arranged for each of the eight landscape elements (Sites 1-8).	299
Table 4.23:	Sum of the number of individuals of carabid and cicindelid species as code numbers (see Table 4.1 for actual names) recorded for the two sampling seasons (June 1994 -May 1996), arranged for each of the eight landscape elements (Sites 1-8).	300
Table 4.24:	Number of individuals of carabid and cicindelid species (sp.) as code numbers (see Table 4.1 for actual names) recorded over the first sampling season (June 1994 - May 1995), for the whole sampling area, arranged for each of the 32 point habitats, for the eight sites (S1-S8). Total abundance (Tot. Abu.); Total number of species (Tot. No. Sp.) 	301
Table 4.25:	Number of individuals of carabid and cicindelid species (sp.) as code numbers (see Table 4.1 for actual names) recorded over the second sampling season (June 1995 - May 1996), for the whole sampling area, arranged for each of the 32 point habitats, for the eight sites (S1-S8). Total abundance (Tot. Abu.); Total number of species (Tot. No. Sp.). 	303
Table 4.26:	Sum of the number of individuals of carabid and cicindelid species (sp.) as code numbers (see Table 4.1 for actual names) recorded over the two sampling seasons (June 1994 - May 1996), for the whole sampling area, arranged for each of the 32 point habitats, for the eight sites (S1-S8).	

Total abundance (Tot. Abu.); Total number of species (Tot. No. Sp.).
 305

Table 4.27: Diversity indices of the eight sites, over the first sampling season (1994/1995), second sampling season (1995/1996) and sum of the two seasons (1994-1996). Margalef's index (R1), Shannon's index (H'), Pielou's evenness index (J'), Simpson's index (λ), Hill's diversity numbers (N1) and (N2). 104

Table 4.28: Diversity indices of the 32 point habitats of the eight sites (S1-S8), over the first (1st) sampling season (1994/1995), second (2nd) sampling season (1995/1996) and sum of the two seasons (1994-1996). Margalef's index (R1), Shannon's index (H'), Pielou's evenness index (J'), Simpson's index (λ), Hill's diversity numbers (N1) and (N2). 105

Table 4.29: Summary of information on cumulative number of species obtained from Tables 4.2-4.20 and Fig. 4.1 (a) (b) (c), for the whole study period. The first sampling season is June 1994-May 1995. The second sampling season is June 1995-May 1996. Column six lists the number of additional new species caught over autumn/winter. Numbers in brackets are species code numbers, see Table 4.1 for actual names of species 117

Table 4.30: V statistic that compares observed diversity (H') with that predicted from Caswell's neutral model for each of the eight sites. The V statistic was calculated using data over the first sampling season (June 1994-May 1995), the second sampling season (June 1995-May 1996) and sum of the two seasons (June 1994-May 1996). 117

Table 4.31(a): Rarefaction model for comparison of species richness between the eight sites (S1-S8), over the first season, second season and sum of the two seasons based on a standard sample size of n=5, n=15 and n=35 respectively 118

Table 4.31(b):	Comparison of three species richness indices namely rarefaction model obtained from Table 4.31(a), Margalef's Index (R1) obtained from Table 4.27 and the theoretical number of species (S*) from the lognormal model (Table 4.32). 119
Table 4.32:	Summary of values calculated from fitting the lognormal to the species data for each of the eight sites (1-8), and to the species data for the whole study area. At Site 6, $a = 0$, therefore, it is not possible to calculate S*. 119
Table 4.33:	Species determining the observed sample (site) patterns, i.e. good discriminators of groups produced by cluster analysis (Fig. 4.9), and MDS analysis (Fig. 4.10). These results were obtained using the program <i>simper</i> (similarity percentages) in PRIMER, which calculates contribution from each species to the separation of pairs of clusters as average similarity within a group and average dissimilarity between groups. Species are shown as code numbers in column five, refer to Table 4.1 for actual names of species 146
Table 4.34:	Combinations of eight environmental variables listed in the second row (K1), taken at level K1 (individually) to K8 (combinations of eight variables e.g 1-5,6,7,8), and the resulting weighted Spearman rank correlation value ρ_w shown in brackets, that measures the degree of matches between biotic and abiotic similarity matrices. Bold type indicates overall optimum match. Bio-env in PRIMER was used 146
Table 4.35:	Ordination results of CA (at the landscape level and at the point habitat level within sites) and CCA produced by running CANOCO, using species data as sum of two seasons (June 1994-May 1996), first sampling season (June 1994-May 1995) and second sampling season (June 1995-May 1996). Numbers 1-17 in the first column, are combinations of environmental variables listed in Chapter 3, Section 3.3.4. Highly

significant gradients are shown with (***) 153

Table 4.36: Basic statistics carried out using MINITAB-ANOVA, showing mean body size (\bar{x}) of carabid and cicindelid species assemblages in each of the eight sites (S1 - S8), arranged in order of increasing body size which is also the order of increasing intensity of disturbance. The mean values of body sizes are significantly different ($P=0.04$) 181

Table 5.1: List of sampling methods of some studies similar to the one here, but carried out in the northern hemisphere, in visually-similar habitats (forests and grasslands) to determine the response of carabids to anthropogenic disturbances 225

LIST OF FIGURES

Figure 2.1(a):	An altitudinal-gradient transect running across two distinct geographical zones (EscarPMENT and Savanna) situated 20 kilometres apart in the vicinity of Pietermaritzburg city, South Africa. The transect runs through four grassland and four forest landscape elements (sites S1-S8), with each landscape element (site) consisting of four point habitats shown as dots. Point habitats were situated at various distances apart (10 metres to about 500 metres) within and among sites 18
Figure 2.1(b):	Schematic map of the study area showing the position of the different landscape elements (sites) relative to each other in the EscarpMENT and Savanna Zones, namely, mistbelt <i>Podocarpus</i> forest under nature management (S1), pine plantation (S2), a park (S3), road verge grasslands (S4) and (S6), <i>Acacia</i> -dominated woodland under nature management (S5), a grassland field (S8). The dots are four point habitats sampled per each of the eight sites 19
Figure 2.1(c):	Actual map of the localities of study sites (three nature reserves) as Ferncliffe nature reserve, World's view nature reserve and Bisley nature reserve 20
Figure 2.2:	Site 1-A mistbelt mixed <i>Podocarpus</i> forest, a primary natural forest with many indigenous tree species under nature management. It is situated in the EscarpMENT Zone at high elevation 30
Figure 2.3:	Site 2-Pine plantation (<i>Pinus patula</i>) in the mid-successional stage, an introduced secondary forest pruned once in August during the first sampling season. It is situated in the EscarpMENT Zone at high elevation 30
Figure 2.4:	Site 3-A recreational park grassland with a lawn kept mown throughout

the year but having some indigenous tree species in addition to lemon and guava trees and ornamental flowers. It is situated in the Escarpment Zone at high elevation 31

Figure 2.5: Site 4-A road verge grassland with autumn burning as a City Council management strategy of preventing accidental fires and bush encroachment. Grass is also cut along a narrow strip of 5 metres wide under electricity posts as a maintenance routine. It is situated in the Escarpment Zone at high elevation.. . . . 31

Figure 2.6: Site 5-*Acacia*-dominated thornveld woodland, a primary natural forest under nature management and Site 6 is a road verge grassland under autumn burning management situated in the same Savanna Zone at lower elevation 32

Figure 2.7: Site 7-A macadamia plantation under agricultural management-irrigation, fertilizers, pesticides, pruning situated in the Savanna Zone at lower elevation 32

Figure 2.8: Site 8-A grassland field with grass mown once a year bordering macadamia plantation situated in the Savanna Zone at lower elevation 33

Figure 3.1(a): Cross-section through a pitfall trap. (a)-Opening into trap, (b)- PVC roof 15 cm by 11 cm by 7 cm with openings into trap from four sides, (c)- Ground level, (d)-Holes in the trap 1 mm in diameter to let out flood water, (e)-An inner trap as a plastic drink cup with a mouth diameter of 7.5 cm and 240 ml capacity, (f)-earth, (g)-collecting fluid as one part ethylene glycol and one part water, (h)-outer jar as a plastic container inserted into the earth to hold the inner cup. It has a hole at the bottom to let out any flood water that overflows from the inner cup. . . . 36

Figure 3.1(b): The three components that make up the pitfall trap. From left to right is the plastic drink cup that makes up the inner trap; a plastic jar that makes

	the outer container which holds the inner trap; a PVC guttering cut in a table shape and used as a roof over the trap	36
Figure 3.2:	A point habitat comprising a set of four pitfall traps at the corners	41
Figure 4.1:	(a) Cumulative number of species recorded over two sampling seasons (June 1994 - May 1995) and (June 1995 - May 1996), for the whole sampling area. (b) Cumulative number of species recorded over the first sampling season (June 1994 - May 1995) and the second sampling season (June 1995 - May 1996) for the whole sampling area	62
Figure 4.1(c):	Cumulative number of species recorded over the first sampling season (June 1994-May 1995) and the second sampling season (June 1995-May 1996), shown for each of the eight sites (1-8).	63
Figure 4.2 (a-f):	Rainfall patterns, with average annual rainfall shown in brackets over the, (a) Escarpment Zone and (d) Savanna Zone. Number of individuals of carabids and cicindelids across twenty four monthly sampling replicates from June 1994-May 1996, is shown for sites within the Escarpment Zone as S1, S2, S3, S4 (b, c) and within the Savanna Zone as S5, S6, S7, S8 (e, f). Total number of individuals collected per site over the whole sampling period is shown in brackets, e.g S1(129). Months over the second sampling season are shown with the number 2, e.g. J2.	65
Figure 4.2(g):	Proportional abundance of carabids and cicindelids recorded over the first sampling season (June 1994-May 1995), the second sampling season (June 1995-May 1996) and as the sum of the two seasons (June 1994-May 1996), arranged for each of the twelve monthly replicates, for the whole sampling area	77
Figure 4.3(a):	Number of species of carabids and cicindelids recorded over the first sampling season (June 1994 - May 1995) and the second sampling season (June 1995 - May 1996) for each of the eight sites (1-8).	78
Figure 4.3(b):	Proportional number of species of carabids and cicindelids recorded over	

the first sampling season (June 1994-May 1995), the second sampling season (June 1995-May 1996) and as the sum of the two seasons (June 1994-May 1996), arranged for each of the twelve monthly replicates, for the whole sampling area 79

Figure 4.3 (c): PCA analysis of the succession of the sampling periods (months) throughout the year using data as sum of two years (June 1994 - May 1996), showing the occurrence of species over months in a primary indigenous forest (Site 1). Individual species are shown by code numbers (e.g. 115a) and represented by an oblique axis (see Table 4.1 for actual species names). The numbers, 1-12 in bold type represent months in a year, e.g. January is 1 and December is 12. 83

Figure 4.3 (d): PCA analysis of the succession of the sampling periods (months) throughout the year using data as sum of two years (June 1994 - May 1996), showing the occurrence of species over months in a pine plantation (Site 2). Individual species are shown by code numbers (e.g. 115a) and represented by an oblique axis (see Table 4.1 for actual species names). The numbers, 1-12 in bold type represent months in a year, e.g. January is 1 and December is 12. 84

Figure 4.3 (e): PCA analysis of the succession of the sampling periods (months) throughout the year using data as sum of two years (June 1994 - May 1996), showing the occurrence of species over months in a recreational park grassland (Site 3). Individual species are shown by code numbers (e.g. 115a) and represented by an oblique axis (see Table 4.1 for actual species names). The numbers, 1-12 in bold type represent months in a year, e.g. January is 1 and December is 12. 85

Figure 4.3 (f): PCA analysis of the succession of the sampling periods (months) throughout the year using data as sum of two years (June 1994 - May 1996), showing the occurrence of species over months in a road verge grassland at high elevation (Site 4). Individual species are shown by code

numbers (e.g. 115a) and represented by an oblique axis (see Table 4.1 for actual species names). The numbers, 1-12 in bold type represent months in a year, e.g. January is 1 and December is 12 86

Figure 4.3 (g): PCA analysis of the succession of the sampling periods (months) throughout the year using data as sum of two years (June 1994 - May 1996), showing the occurrence of species over months in a Savanna *Acacia*-dominated woodland (Site 5). Individual species are shown by code numbers (e.g. 115a) and represented by an oblique axis (see Table 4.1 for actual species names). The numbers, 1-12 in bold type represent months in a year, e.g. January is 1 and December is 12 87

Figure 4.3 (h): PCA analysis of the succession of the sampling periods (months) throughout the year using data as sum of two years (June 1994 - May 1996), showing the occurrence of species over months in a road verge grassland at low elevation (Site 6). Individual species are shown by code numbers (e.g. 115a) and represented by an oblique axis (see Table 4.1 for actual species names). The numbers, 1-12 in bold type represent months in a year, e.g. January is 1 and December is 12 88

Figure 4.3 (i): PCA analysis of the succession of the sampling periods (months) throughout the year using data as sum of two years (June 1994 - May 1996), showing the occurrence of species over months in a macadamia plantation (Site 7). Individual species are shown by code numbers (e.g. 115a) and represented by an oblique axis (see Table 4.1 for actual species names). The numbers, 1-12 in bold type represent months in a year, e.g. January is 1 and December is 12 89

Figure 4.3 (j): PCA analysis of the succession of the sampling periods (months) throughout the year using data as sum of two years (June 1994 - May 1996), showing the occurrence of species over months in a field of hay (Site 8). Individual species are shown by code numbers (e.g. 115a) and represented by an oblique axis (see Table 4.1 for actual species names).

The numbers, 1-12 in bold type represent months in a year, e.g. January is 1 and December is 12 90

Figure 4.3 (k): PCA analysis of the succession of the sampling periods (months) throughout the year using data as sum of two years (June 1994 - May 1996), showing the occurrence of species over months in the whole study area. Individual species are shown by code numbers (e.g. 115a) and represented by an oblique axis (see Table 4.1 for actual species names). The numbers, 1-12 in bold type represent months in a year, e.g. January is 1 and December is 12 91

Figure 4.4: (a) Total number of individuals (4197), (b) total number of species (35), recorded over the whole study area, over two years (June 1994-May 1997), and shown proportionally for each of the eight sites (S1-S8) 95

Figure. 4.5: Comparison of diversity measures of species richness ($R1$), Shannon's diversity index (H') and Pielou's evenness index (J'), using data as sum of the two sampling seasons (June 1994-May 1996), shown for each of the eight sites (1-8). 102

Figure 4.6(a): Frequency distribution of carabid and cicindelid abundance data, as the sum of two sampling seasons (June 1994-May 1996), plotted in octaves and shown for the whole study area. Observed data is shown as solid squares and fitted lognormal model as a curve. Octaves are classes of individuals (0-1,1-2, 2-4, 4-8, 8-16 etc). The frequency of number of individuals (n) that falls between two octaves is shared.. . . 102

Figure 4.6(b): Frequency distribution of carabid and cicindelid abundance data, as the sum of two sampling seasons (June 1994-May 1996), plotted in octaves and shown for each of the eight sites (1-8). Observed data is shown as solid squares and fitted lognormal model as curves 103

Figure 4.7(a): Plots of x^2 geometric species abundance classes, using data over the first

	sampling season (June 1994-May 1995), shown for each of the eight sites (S1-S8).	121
Figure 4.7(b):	Plots of x2 geometric species abundance classes, using data over the second sampling season (June 1994-May 1996), shown for each of the eight sites (S1-S8).	122
Figure 4.8:	Plots of ranked species abundance (dominance) curves, using data as the sum of two sampling seasons (June 1994-May 1996). Species are ranked in decreasing order of their importance in terms of abundance from most common to most rare, and shown for each of the eight sites (S1-S8)	126
Figure 4.9:	Dendrogram for hierarchical clustering of the eight sites (1-8), using group-average linking of Bray-Curtis similarities calculated on 4th root-transformed abundance data of carabids and cicindelids as sum of two seasons (June 1994-May 1996), using PRIMER.	128
Figure 4.10(a):	MDS ordination of the eight sites (1-8) based on 4th root-transformed abundance data and Bray-Curtis similarities of carabid and cicindelid abundance data as sum of two sampling seasons (June 1994-May 1996), using PRIMER. Stress=0.13.	128
Figure 4.10(b):	MDS ordination of the eight sites (1-8) based on 4th root-transformed abundance data and Bray-Curtis similarities of carabid and cicindelid abundance data over the first sampling season (June 1994-May 1995), using PRIMER. (Stress=0.09).	129
Figure 4.10(c):	MDS ordination of the eight sites (1-8) based on 4th root-transformed abundance data and Bray-Curtis similarities of carabid and cicindelid abundance data over the second sampling season (June 1995-May 1996), using PRIMER. (Stress=0.15).	129
Figure 4.11:	Dendrogram for hierarchical clustering of the 32 point habitats in the	

eight sites, using group-average linking of Bray-Curtis similarities calculated on 4th root-transformed abundance data of carabids and cicindelids as sum of two seasons (June 1994-May 1996), using PRIMER 132

Figure 4.12(a): MDS ordination of the 32 point habitats (1-32) in the eight sites (S1-S8) based on 4th root-transformed abundance data and Bray-Curtis similarities of carabid and cicindelid abundance data as sum of the two sampling seasons (June 1994-May 1996), using PRIMER. (Stress=0.19) 132

Figure 4.12(b): MDS ordination of the 32 point habitats (1-32) over the eight sites based on 4th root-transformed abundance data and Bray-Curtis similarities of carabid and cicindelid abundance data over the first sampling season (June 1994-May 1995), using PRIMER. (Stress=0.01). 133

Figure 4.12(c): MDS ordination of the 32 point habitats (1-32) over the eight sites (S1-S8) based on 4th root-transformed abundance data and Bray-Curtis similarities of carabid and cicindelid abundance data over the second sampling season (June 1995-May 1996), using PRIMER. (Stress=0.15) 134

Figure 4.13: (a) A 2-dimensional PCA ordination of the 17 environmental variables listed in Chapter 3, section 3.3.4, and shown for the eight sites (1-8). Total variance explained by the first two components is 57%. (b) MDS ordination based on species data (biota). 136

Figure 4.14: (a) MDS ordination of carabid and cicindelid species data (biota) of the eight sites (1-8). (b)-(f) is the same MDS but with superimposed circles of increasing size with increasing sand, moisture, pH, shade and litter as quantitative variables at each of the eight sites. Nominal variables specifying a classification of the eight sites are shown in (g) geographical location, (h) habitat type and (i) management regime 137

Figure 4.15: (a) MDS ordination of carabid and cicindelid species data (biota) of the eight sites (1-8). (b)-(f) MDS ordination based on sand, pH, moisture, litter and shade as quantitative variables. MDS ordination based on nominal variables specifying a classification of the eight sites shown as, (g) geographical location, (h) habitat type and (i) management regime
 141

Figure 4.16: (a) MDS ordination of carabid and cicindelid species data (biota) of the eight sites (1-8). (b) is PCA of all 17 environmental variables listed in Chapter 3, section 3.3.4. (c)-(i) MDS ordination based on combinations of environmental variables listed in section 3.3.4 as sand, pH, moisture, litter and shade (1-5); geographical location (6), habitat type (7); management regime (8). Numbers in brackets are Spearman's rank correlation values ρ_w 144

Figure 4.17: Ordination diagram of correspondence analysis (CA), using carabid and cicindelid species data as sum of two sampling seasons, June 1994-May 1996 (Table 4.23). The first axis $\lambda_1=0.691$ is horizontal and the second axis $\lambda_2=0.620$ is vertical. The diagram shows the distribution of species among the eight sites (1-8 shown in bold type numbers). Species are shown in small type numbers following the order of listing in Table 4.23. CANOCO was used. 149

Figure 4.18: Ordination diagram of canonical correspondence analysis (CCA), using data as sum of two sampling seasons (June 1994-May 1996). It is based on five environmental variables of soil characteristics 1-5, listed in Section 3.3.4. The diagram shows the distribution of carabid and cicindelid species among the eight sites (1-8 in bold type numbers), and along environmental variable gradients (oblique axis). Species are shown in small type numbers following the order of listing in Table 4.23. The first axis $\lambda_1=0.675$ is horizontal and the second axis $\lambda_2=0.565$ is vertical
 151

Figure 4.19: Ordination diagram of canonical correspondence analysis (CCA), using data as sum of two sampling seasons (June 1994-May 1996). It is based on four environmental variables of soil characteristics 1-4, listed in Section 3.3.4. The diagram shows the distribution of carabid and cicindelid species among the eight sites (1-8 in bold type numbers), and along environmental variable gradients (oblique axis). Species are in small type numbers following the order of listing in Table 4.23. The first axis $\lambda_1=0.672$ is horizontal and the second axis $\lambda_2=0.559$ is vertical

. 154

Figure 4.20: Ordination diagram of canonical correspondence analysis (CCA), using data as sum of two sampling seasons (June 1994-May 1996). It is based on environmental variables of soil characteristics 1-4 and geographical location 6-7, listed in Section 3.3.4. The diagram shows the distribution of carabid and cicindelid species among the eight sites (1-8 in bold type numbers), and along environmental variable gradients (oblique axis). Species are in small type numbers following the order of listing in Table 4.23 156

Figure 4.21: Ordination diagram of canonical correspondence analysis (CCA), using data as sum of two sampling seasons (June 1994-May 1996). It is based on environmental variables of habitat type 8-11, listed in Section 3.3.4. The diagram shows the distribution of carabid and cicindelid species among the eight sites (1-8 in bold type numbers), and along environmental variable gradients (oblique axis). Species are in small type numbers following the order of listing in Table 4.23. The first axis $\lambda_1=0.503$ is horizontal and the second axis $\lambda_2=0.371$ is vertical . . . 158

Figure 4.22: Ordination diagram of canonical correspondence analysis (CCA), using data as sum of two sampling seasons (June 1994-May 1996). It is based on environmental variables of management regime 12-17, listed in Section 3.2.4. The diagram shows the distribution of carabid and

cicindelid species among the eight sites (1-8 in bold type numbers), and along environmental variable gradients (oblique axis). Species are in small type numbers following the order of listing in Table 4.23. The first axis $\lambda_1=0.641$ is horizontal and the second axis $\lambda_2=0.502$ is vertical

. 160

Figure 4.23: Ordination diagram of canonical correspondence analysis (CCA), using data as sum of two sampling seasons (June 1994-May 1996). It is based on environmental variables of soil characteristics 2, 3, 4 and management regime 12, 15, 16, listed in Section 3.2.4. The diagram shows the distribution of carabid and cicindelid species among the eight sites (1-8 in bold type numbers), and along environmental variable gradients (oblique axis). Species are in small type numbers following the order of listing in Table 4.23. The first axis $\lambda_1=0.689$ is horizontal and the second axis $\lambda_2=0.618$ is vertical 162

Figure 4.24: Ordination diagram of correspondence analysis (CA), using carabid and cicindelid species data over the first sampling seasons, June 1994-May 1995 (Table 4.21). The first axis $\lambda_1=0.764$ is horizontal and the second axis $\lambda_2=0.575$ is vertical. The diagram shows the distribution of species among the eight sites (1-8 in bold type numbers). Species are shown as code numbers in small type following the order of listing in Table 4.21. CANOCO was used 163

Figure 4.25: Ordination diagram of canonical correspondence analysis (CCA), using carabid and cicindelid species data over the first sampling seasons, June 1994-May 1995 (Table 4.21). It is based on environmental variables of soil characteristics 2, 3, 4 and management regime 12, 15, 16, listed in Section 3.3.4. The diagram shows the distribution of carabid and cicindelid species among the eight sites (1-8 in bold type numbers), and along environmental variable gradients (oblique axis). Species are shown as code numbers in small type following the order of listing in Table 4.21.

The first axis $\lambda_1=0.750$ is horizontal and the second axis $\lambda_2=0.571$ is vertical 165

Figure 4.26: Ordination diagram of correspondence analysis (CA), using carabid and cicindelid species data over the second sampling seasons, June 1995-May 1996 (Table 4.22). The first axis $\lambda_1=0.737$ is horizontal and the second axis $\lambda_2=0.688$ is vertical. The diagram shows the distribution of species among the eight sites (1-8 in bold type numbers). Species are shown as code numbers in small type following the order of listing in Table 4.22. CANOCO was used 166

Figure 4.27: Ordination diagram of canonical correspondence analysis (CCA), using carabid and cicindelid species data over the second sampling seasons, June 1995-May 1996 (Table 4.22). It is based on environmental variables of soil characteristics 2, 3, 4 and management regime 12, 15, 16, listed in Section 3.3.4. The diagram shows the distribution of carabid and cicindelid species among the eight sites (1-8 in bold type numbers), and along environmental variable gradients (oblique axis). Species are shown as code numbers in small type following the order of listing in Table 4.22. The first axis $\lambda_1=0.736$ is horizontal and the second axis $\lambda_2=0.662$ is vertical 168

Figure 4.28: Ordination diagram of correspondence analysis (CA) of carabid and cicindelid species data at the point habitat level, using data as sum of two sampling seasons, June 1994-May 1996, (Table 4.26). The first axis $\lambda_1=0.735$ is horizontal and the second axis $\lambda_2=0.678$ is vertical. The diagram shows the distribution of species among the 32 point habitats of the eight sites (S1-S8). Species are shown in small type numbers following the order of listing in Table 4.26. CANOCO was used . . 169

Figure 4.29: Ordination diagram of principal components analysis (PCA) of carabid and cicindelid species data at the point habitat level, using data over the first sampling season, June 1994-May 1995, (Table 4.24). The first axis

$\lambda_1=0.583$ is horizontal and the second axis $\lambda_2=0.108$ is vertical. The diagram shows the distribution of species among the 32 point habitats of the eight sites. Species are shown by oblique axis in small type numbers, using code numbers listed in Table 4.24. CANOCO was used . . . 172

Figure 4.30:

Ordination diagram of correspondence analysis (CA) of carabid and cicindelid species data at the point habitat level, using data over second sampling season, June 1995-May 1996, (Table 4.25). The first axis $\lambda_1=0.823$ is horizontal and the second axis $\lambda_2=0.788$ is vertical. The diagram shows the distribution of species among the 32 point habitats of the eight sites. Species are shown as code numbers in small type following the order of listing in Table 4.25. CANOCO was used

. 174

Figure 4.31:

Ordination diagram of correspondence analysis (CA) at the point habitat level of two grassland road verges (as S4, with point habitats 13-14 and S6, with point habitats 21-24 shown in bold type numbers), using carabid and cicindelid species data over the first sampling season, June 1994-May 1995, (Table 4.24). The diagram shows the distribution of species among the eight point habitats of the two sites. Species are shown as code numbers in small type following the order of listing in Table 4.24

. 176

Figure 4.32:

Ordination diagram of correspondence analysis (CA) at the point habitat level of two grassland road verges (as S4, with point habitats 13-14 and S6, with point habitats 21-24 shown in bold type numbers), using carabid and cicindelid species data over the second sampling season, June 1995-May 1996, (Table 4.25). The diagram shows the distribution of species among the eight point habitats of the two sites. Species are shown as code numbers in small type following the order of listing in Table 4.25

. 177

CHAPTER 1

INTRODUCTION

1.1 THE MACROECOLOGICAL APPROACH

The world biota is declining at an accelerating rate (May *et al.*, 1995). This is especially so for insects (Mawdsley and Stork, 1995; Samways, 1996). Recent years have seen the emergence of macroecology as a distinct research programme in biology which is concerned with geographical-scale patterns in assemblage structure, and as such, relies on approaches that are nonexperimental and that depend on the availability of reliable information for large numbers of species (Brown, 1995; Blackburn and Gaston, 1998). Macroecology provides a useful theoretical background for studying human-induced landscape changes on a global scale. It is a useful approach for identifying transregional and interregional differences as to how assemblages change. For instance, studies in Finland and Canada (Niemela *et al.* 1993) have shown the feasibility of a multi-regional approach. These studies show that, the general patterns of community response to human caused disturbances are surprisingly similar.

The macroecological approach can also be used as a management tool distinguishing between local effects and general global effects. For example, in Europe, only small sized carabid species survive frequent disturbance (Sustek 1992; Blake *et al.* 1996). Another example is the similar effects of forestry on carabid communities in the Palaearctic and Nearctic forests (Niemela *et al.* 1994). Also in soil decomposer animal communities, general and common responses to anthropogenic disturbance have been found (Salminen and Haimi 1996).

These examples illustrate global trends indicating that it may be possible to develop management and conservation practices that could be applicable in various parts of the world. However, as species composition differ, conservation and appropriate management cannot be applied globally. However, because macroecological studies also have predictive value, knowing that particular

human activities have particular effects everywhere means that we know the outcome of our actions. And although local effects cannot be predicted, it is the macroecological aim to tease apart these effects of scale (Niemela, Kotze, Ashworth, Brandmayr, Desender, New, Penev, Samways, Spence and Wright - personal communication).

The relevance of macroecology to this study is that a standard methodology developed in one part of the world can be deployed in another part to give comparable results (Blackburn and Gaston, 1998). To achieve this, data must be gathered at different locations, yet using the same methodological yardsticks.

1.2 LANDSCAPE DISTURBANCE FACTORS AND BIOINDICATORS

Landscape ecology recognises that humans are an integral part of the environment. It studies the ecological implications of the dynamic interrelationships between humans and their open and built up landscapes. Any comprehensive, physiographic or integrated approach to the survey of separate land elements makes use of landscape ecology (Naveh and Lieberman, 1984). The landscape element or ecosystem is any holistic unit of the landscape, the size of which is determined by the scale of dissection of the landscape (Samways, 1994). The selection of the appropriate scale is critical, and will be determined by the aims of the study.

Disturbances may be small and localized over a few metres, or widespread, natural or a human-induced disruption changing the appearance of the landscape. Disturbance has been described by White and Pickett (1985) as a relatively discrete event in time that disrupts ecosystems, community or population structure and changes resources, substrate availability or the physical environment. Such disruptions may vary in distribution, frequency, predictability and severity. They may be synergistic with other disturbances (Myers, 1993), such as long periods of drought, or may increase the risk of a fire outbreak, or range changes in response to elevated global temperatures (Harrington and Stork, 1995).

Pimm (1986) has pointed out that most of the earth is disturbed and dominated neither by pristine ecological communities nor by species on the brink of extinction. The ecological communities are fragmented, harvested and polluted owing to the disturbance stresses caused by humans (Samways,

1994, 1996). As insects are a major component of landscapes, both as individuals and as species, it is likely that any landscape disturbances have a major impact on their population levels, patterns and distributions. Yet, in insect conservation biology, little is known of how the relative abundances of insects change with disturbance in landscapes (Lawton *et al.*, 1998), except mostly through some detailed autecological and pollution studies, with a bias towards aquatic invertebrates, (Winner *et al.*, 1980; Hellawell, 1986; Rosenberg and Resh, 1993; Clarke and Warwick, 1994; Chessman, 1995).

1.2.1 Bioindicators

The use of bioindication in biological conservation and evaluation studies for terrestrial systems, particularly using invertebrate indicators, has gained momentum only within the last two decades (Holloway, 1980; Holloway and Stork, 1991; Stork and Eggleton, 1992; Stork, 1994; Stork and Samways, 1995; Luff and Woiwod, 1995; Niemela, 1997). Therefore, far more data are required to understand the response of terrestrial insects to disturbance, so that better management strategies can be put in place to conserve them.

Recently, McGeoch (1998), has reviewed the selection, testing and application of terrestrial insects as bioindicators. She has pointed out that in the majority of studies carried out on the uses and merits of terrestrial insects as indicators there is a lack clear definition, goals and hypothesis testing in the field. Questions concerning the protocols that should be used to identify indicator taxa and whether or not they can be designated objectively have also been raised (Stork and Samways, 1995). It has even been suggested that the basis for insect indicator selection is often merely based on favoured or convenient taxa (Soulé and Kohm, 1989; Woiwod and Thomas, 1993; Williams and Gaston, 1994). Many authors have listed *a priori* criteria for the selection of potentially effective insect indicator taxa (e.g. Holloway and Stork, 1991; Pearson, 1994) and many studies have applied these criteria (Pearson and Cassola, 1992). However, these taxa are just potentially suitable and have not been tested and applied as indicators. Only a few studies adopt the rigorous testing approach advocated in McGeoch, (1998), (e.g. Dallinger *et al.*, 1992; Balmford *et al.*, 1996a,b.; Paoletti *et al.*, 1995; Samways and Steytler, 1996). The only potential addition to some of these studies (e.g. Paoletti *et al.*, 1995; Samways and Steytler, 1996), as pointed out by McGeoch (in

press), would be the generalisation of the results found (by testing on independent data set) and the provision of a geographical range estimate within which the selected bioindicators may be used. This study therefore, aims to use the macroecological approach. It researches a local situation, and then compares the distribution patterns and response of carabid and cicindelid beetles to landscape disturbances in the northern and southern hemispheres. The present knowledge and data on ground beetles are heavily biased towards species living in the north-temperate regions (Stork, 1990; Lovei and Sunderland, 1996; Niemela, 1996a). This is a limiting factor in the testing of ground beetles for their value as biological indicators on a global scale (Eyre *et al.*, 1996). This is the first study to report the distribution patterns and responses to landscape disturbances of these animals in southern Africa.

1.2.2 Intermediate disturbance hypothesis

Increasing levels of environmental stress have generally been considered to decrease diversity (H'), i.e. decrease species richness and decrease evenness (J') which increases dominance. Recent theories on the influence of disturbance or stress on diversity suggest that in situations where disturbance is minimal, species diversity is reduced because of competitive exclusion between species. With a slightly increased level or frequency of disturbance competition is relaxed, resulting in an increased diversity, and then at still higher or more frequent levels of disturbance species start to become eliminated by stress, so that diversity falls again. Thus it is at intermediate levels of disturbance that diversity is highest (Connell, 1978; Huston, 1979). Therefore, depending on the starting point of the community in relation to existing stress levels, increasing levels of stress (e.g. induced by pollution) may either result in an increase or decrease in diversity. It is difficult if not impossible, to say at what point on this continuum the community under investigation exists, or what value of diversity one might expect at that site if the community were not subjected to any anthropogenic stress. Thus, changes in diversity can only be assessed by comparisons between points along a spatial contamination gradient or with historical data.

1.2.3 Burning

Natural burns on the landscape from lightening strikes are a widespread phenomenon, particularly

in savanna areas such as parts of Australia and Africa (Gill *et al.*, 1981). Burning maintains the savanna as grassland, preventing succession to natural scrub (Tainton and Mentis, 1984). Currently, many management strategies for grasslands, woodland and forests do not take the invertebrate fauna into consideration (Morris, 1971, 1991; Vane-Wright *et al.*, 1991, 1994; Greenslade, 1997; Samways, 1996). Therefore, the invertebrate fauna must be well known, taxonomically, and ecologically, if its consideration is to be a factor in management of habitats for wildlife conservation. At present, very little is known of the invertebrate faunas of grassland, woodland and forest and how they respond to various disturbances or management. It is important to appreciate that the effects of management, or of ceasing to manage, habitats, influence different plant species at very different rates (Morris, 1971, 1991). In turn, this has direct or indirect effects on invertebrates associated or dependent on them (Myers, 1993; Samways, 1996).

Although some Australian plant communities are adapted to fire, the frequency, timing and intensity of burning influences the rate of recovery of structure and function to the prefire state (Cheal, 1996; Tolhurst, 1996). Too frequent fires, or, a total absence, are both likely to result in loss of invertebrate species (York, 1996; Lowe, 1995), plant species, (Prober, 1995) and the community type, will differ depending on the interval between burns (Gill, 1996). Holliday (1991, 1992) in Canada showed that several carabid species (and other insects) require burnt organic material. Due to the virtual absence of forest fires in Sweden resulting from effective fire prevention (Wikars, 1995), many species have declined, and at least one carabid (*Agonum bogemanni* Dej.) has probably gone nationally extinct in Sweden (Wikars, 1992).

The aim of most fuel reduction burning is to reduce the risk of wild fire, so the optimal conditions required for different plant communities are not considered (Gill, 1996). It is now increasingly recognised however, that fire management plans should be based on knowledge of the responses of all components of the fauna and flora to burning, so that as much of the biodiversity of the ecosystem as possible can be preserved (Anon, 1992).

Fire management plans which protect floristic diversity and vegetation type will not necessarily protect invertebrate diversity, since invertebrates respond to abiotic factors differently from plants. The assumption that if all habitats are conserved, then all invertebrates are conserved is generally

well founded (Cho *et al.*, 1995). However, this assumption has been shown by a number of studies to be false (Greenslade and New, 1991; Greenslade, 1997). Until the invertebrate fauna has been surveyed and macro- and microhabitats requirements determined, any fire management plan based on vegetation communities alone cannot guarantee conservation of the invertebrate fauna.

Friend (1996) and Greenslade *et al.* (1996), have reviewed the effects of fire on invertebrates. In many studies on the effects of wild fires and prescribed burns on invertebrates in Australia, identification has been to the level of order (Neumann and Tollhurst, 1991; Abbott, 1984; Coy, 1996; Hutson and Kirkby, 1985) and these studies have tended to show a rapid recovery in abundance and representation of all orders after fire. Moreover, some studies indicate that invertebrate responses to season and site were greater than to the fire itself (Friend, 1996). Consequently some authors have concluded that the effect on invertebrates of prescribed burning is short term and insignificant (Abbot *et al.*, 1984; Neumann and Tolhurst, 1991). This study here focusses on carabids and cicindelids at the species level, with the aim of determining their specific responses to prescribed fire management in grasslands of road verges.

A high proportion of the studies have been on ants (Majer, 1980; Andersen and Yen, 1985), a group which generally has a preference for open habitats and high temperatures (Greenslade, 1997), which is not typical of the responses of invertebrates of more humid habitats (such as ground beetles) to fire. Other higher taxa which could be appropriate 'indicators' of fire effects were recommended by Friend (1996). He concluded that five higher taxa were 'sensitive' to fire. These were Araneae, Lepidoptera, Isoptera, Isopoda, Blattodea and Thysanura. However, Isopoda, Blattodea and Thysanura are not usually present in high enough numbers for data on them to be sufficiently informative (Greenslade, 1997). The taxonomic difficulties and high diversity of Araneae make their use as an 'indicator group' problematical, and the problems in sampling Lepidoptera quantitatively are well known. Greenslade and Rosser (1984) and Coy (1996) showed that Dermaptera and Amphipoda respectively were very sensitive to fire in having high abundances before burning and not having returned for a year after the burn. Where present, they are clearly taxa to be considered as candidates for 'indicators'.

Fire can also affect decomposition processes. For instance, by reducing populations of litter

decomposing invertebrates, fire can, even in the short term, result in a more rapid build up of fuel after a prescribed burn because of reduced rates of decomposition. Hodda (1991) found fewer and smaller harvester termite mounds in annually burnt areas compared to unburnt areas. In annually burnt areas, there was also a reduced loss of leaf litter compared to unburnt areas and this was directly linked to a slower rate of removal of plant material by termites.

It has been shown that species composition of faunas from plant communities of different ages since the fire can differ markedly (Friend and Williams, 1993-beetles; Little and Friend, 1993-spiders; Abensperg-Traun and Milewski, 1995-termites; Hodda, 1991-termites; Greenslade, 1994-springtails). These differences in composition can persist for many years after the fire. Moreover, there is some evidence to show that inappropriate fire regimes can cause local extinctions of some species (Lowe, 1995) and, in eucalypt forest, York (1994, 1996) has shown that there is a suite of fire sensitive ant species which are lost from areas under an intensive burning regime. It is therefore essential to identify the fauna to species and morphospecies to adequately demonstrate the real effect of fire on invertebrate communities (Greenslade, 1997).

1.2.4 Road verges and prescribed autumn burning disturbance

Eversham *et al.* (1996) have shown that urban, industrial and other man-made sites are serving as analogues of natural habitats for carabids. Examples of natural habitats and their manmade analogues respectively are, heathland=abandoned sand/gravel pits; sand-dune=perpetually disturbed road-verges on sandy soil and also active sand/gravel pits; open woodland=hedgerows; fenland=wetlands on pulverised fuel ash from power stations or flooded sand quarries. Man-made sites are comparatively recent origin. They generally support a proportion of eurytopic species which occur in the surrounding landscape, and a stenotopic (rare and threatened) component comprising colonists from semi-natural habitats (Eversham *et al.*, 1996). Several studies have found interesting assemblages of carabids in manmade sites (Lazenby, 1983; Harding *et al.*, 1988; Eversham, 1992; Eversham and Telfer, 1994; Lott and Daws, 1994; Eyre and Luff, 1994a). Survival of species once they have reached man-made sites will depend on how closely the site matches the environmental conditions of the semi-natural equivalent. The role of human activity in extending or maintaining the geographic range of thermophilous species in the post-glacial period has been

postulated by Thomas (1993). In Britain, man-made habitats support a rich carabid fauna, including 35% of the rare and scarce species. They represent one of the few habitats which is increasing in area within Britain (Eversham *et al.*, 1996). Roads and railways have the potential both to divide and fragment semi-natural habitats, but also to link them (Vermeulen, 1993; Eversham and Telfer, 1994). Many sites are currently derelict, and nature conservation would provide an inexpensive after-use. Some of the habitats which are easily maintained in man-made sites, such as road verges, by a low level of disturbance, such as burning and mowing or cutting, produce bare ground and early-successional stages, and are particularly valuable to carabids (Vermeulen, 1993; Eversham and Telfer, 1994, Eversham *et al.*, 1996). Although their lack of an immediate aesthetic appeal may be an obstacle to acceptance by conservationists and planners (Eyre and Luff, 1994a), these early successional stages are important because they are generally absent or difficult to maintain within traditional nature reserves. Carabids provide an ideal group to sample for monitoring purposes (Eyre *et al.*, 1996), and Eversham *et al.*, (1996) have proposed that by comparing a site with the regional species-pool for the major semi-natural habitats, man-made sites can be judged fairly and objectively.

Within the city of Pietermaritzburg, in South Africa, the city by-laws prescribe the maintenance of grassland and bush along road verges and within nature reserves by controlled burning and /or cutting with the aim of reducing the risk of wild fire and bush encroachment. Within the woodlands and forests of the nature reserves, rotational burning is carried out at five-year intervals. However, along the road verges, especially those bordering the nature reserves, controlled burning is carried out every year in autumn in the sites situated in the zone with savanna hot climate, and every other year in the sites situated in the zone with an escarpment cool climate. This management strategy has been adopted from the management routines of the major national game reserves in the country, whose management strategies are biased towards the conservation of large vertebrates and plants. In the current management of these road verges, invertebrates are not considered at all. Therefore, this study aims to monitor the response of carabids and cicindelids to the management disturbances of burning so that they can be taken in to consideration in management planning. In addition, the study aims to determine whether road verges in the southern hemisphere have high potential for conservation value as has been proposed by Eversham *et al.* (1996) in the northern hemisphere.

1.2.5 Mowing

Cutting differs from grazing in a number of respects, but as far as defoliation is concerned, the chief difference is in the non-selectivity of the mowing machine and the fact that it produces a sward of uniform height, whereas grazing is selective and, unless very intensive, produces a patchy vegetation (Morris, 1971). Southwood and Van Emden (1967) found more animals on cut grass than on the uncut, although biomass was generally slightly greater on the uncut grass. For many taxonomic groups, e.g. Araneae, Acarina, Collembola, Homoptera and Coleoptera, more individuals were found on the cut grassland than on the uncut.

The negative effects of overgrazing by domestic animals are well known, particularly because of their increase in recent years (Goudie, 1989). However, the converse, particularly in temperate areas, has conservation significance for many invertebrates, especially insects (Fry and Lonsdale, 1991). Indeed, various insect species from various groups, such as the Coleoptera and Heteroptera (Morris, 1971), Lepidoptera (Dempster, 1971, Thomas *et al.*, 1986), Orthoptera (Marshall and Haes, 1988) and ants (Samways, 1983), depend on some regular disturbance to maintain their population numbers.

It is the major disturbances such as ploughing, heavy grazing, fertilizing plots, vertebrate grazing, and recreational pressure that contribute to declining population levels, and loss of the local insect populations (Fry and Lonsdale, 1991). Most studies have shown that, for preservation of the greatest number of species, a spatially variable management regimen including rotation mowing (Morris, 1971, 1991) and restoration activities such as increasing flowering herbs (Wells *et al.*, 1989; Ash *et al.*, 1992; Blake *et al.*, 1996), is necessary. However, if the aim is to conserve a population of a particular species, then management will depend on specific pointers from autecological studies. Hence, this study aims to determine how species of carabids and cicindelids respond to mowing disturbances in grasslands.

1.2.6 Woodlands and forests

Primary and old-growth woodland or forests, whether in Europe (Rackham, 1980), North America (Harris, 1984), Australia (New, 1984) or the tropics (Jacobs, 1988), are major climax growth areas

whose fragmentation into patches is to be avoided as it is damaging to interior species (Forman and Gordon, 1986; Niemela, 1997).

Nature reserves alone cannot conserve biological diversity effectively, and barriers to migration make species in reserves especially vulnerable to global climate change (Wilcove, 1989; Westman, 1990). However, reserves can be complemented with a matrix of semi-natural lands where ecological principles are used to manage both for commodity production and conservation of species diversity (Harris, 1984; Hansen *et al.*, 1991).

Although environmental impact assessments (EIA) have been conducted, for example by Mondi Forests, South Africa, before the afforestation of a new area is done (Pott, 1989, 1997), little is known of the actual impact of plantation forestry on biodiversity in South Africa. Even in the northern hemisphere, criticism of boreal forest management has prompted development of methods intended to enhance the maintenance of biodiversity while harvesting timber in a socio-economically acceptable way (Franklin, 1989; Esseen *et al.*, 1992; Bradshaw *et al.*, 1994; Korhonen, 1994; Noss and Cooperrider, 1994). However, due to incomplete knowledge on the ecological effects of current forest practices, the new methods are working hypotheses rather than carefully tested concepts (Franklin, 1995). Niemela (1997) has reviewed the significance of invertebrates in boreal forest management. He points out that a considerable body of information on the effects of forestry on invertebrates has accumulated in the northern hemisphere, and that invertebrates have potential utility as surrogates for biodiversity. Yet insects are not very often used in conservation studies (Franklin, 1993; Kim, 1993; Kremen *et al.*, 1993; Miller, 1993; Loreau, 1994). Niemela (1997) has summarized the main effects of forestry on boreal biota and discussed possible ways of maintaining boreal forest biodiversity while harvesting timber. These recommendations are based on knowledge acquired from species living in the northern hemisphere. Although these recommendations can be adopted by foresters in the southern hemisphere, it is important to ascertain the actual responses of species in this region to forest management and to identify which species are most vulnerable.

1.2.7 Agriculture

Replacement of natural vegetation by an irrigated and fertilized monocrop can cause insect

population surges with loss of other species (Samways, 1996). In the dry savanna of South Africa, islands of citrus produce high resident populations of an indigenous thrips *Scirtothrips aurantii* Faurie (Samways *et al.*, 1987) and a psyllid *Trioza erytrae* Del Guercio (Samways, 1987), while reducing, for example, the epigaeic ant fauna (Samways, 1989b). Such thrips and psyllid populations are notoriously difficult to control biologically, which encourages the use of pesticides, which in turn, is harmful to other insects (e.g. ants in citrus: Samways, 1981). To lessen these discontinuous population upsurges, management approaches have been polycropping (Andow, 1991), chemically untreated headlands (Dover, 1991) and planting of habitat islands to encourage natural predators (Wratten and Van Emden, 1995). The study here partly focuses on a macadamia orchard, in the dry savanna of South Africa, which is under intensive irrigation and fertilization and other agricultural management techniques. The aim is to monitor the response of the invertebrate fauna (with a focus on carabids and cicindelids) to these disturbances, so that management for biodiversity can be put in place.

1.2.8 Seasonal variations

Severe weather conditions from cold snaps in the temperate regions, to rain storms and cyclones in the tropics, sometimes have visible dramatic effects upon patches of vegetation. Inclement conditions that are exceptional in being sudden and severe or prolonged, such as long cool periods or extremely dry ones, can have a major impact upon insect populations, sometimes causing them to fragment into smaller populations (Samways, 1989a, 1994, 1995, 1996). Some insect populations recover remarkably quickly from disturbances that subside fairly quickly e.g Odonata assemblage (Samways, 1989a). In addition to spatial variation, there is temporal variation in insect assemblages on different scales. The season of sampling affects the catches because some species occur in the early season and some later. In addition, there is variation between years, which is more difficult to study as this requires long-term monitoring. In some cases, variation from one year to the next in the same assemblage may be greater than variation in the same year between neighbouring assemblages. For instance, Sanderson (1994) reports that within a farm-level experiment, 47% of the variation in invertebrate assemblages was explained by between year differences and 17% by environmental variation.

This study aims to determine not only spatial distributions of carabid and cicindelid in forest and grassland landscapes, but also to determine the response of these animals to seasonal variations.

1.3 CONSERVATION STRATEGIES FOR INVERTEBRATES

The strategies which have been adopted for vertebrate conservation cannot necessarily be applied to invertebrates. Invertebrate home ranges are generally much smaller (Ehrlich, 1992). Their populations exist at much higher numbers and fluctuate to such an extent that local populations become extinct (Dempster, 1989; Gaston 1994; Lawton and May, 1995). Microhabitats are often more important to insects (Drewett, 1988), which are often dependent upon particular species of plants or hosts and upon particular microclimates, not only as adults but also as larvae (Moore, 1991).

1.4 GROUND BEETLES AS SUBJECTS

Gaston (1991) has pointed out that the family Carabidae, is one of the most diverse families of beetles. This diversity causes problems for classification and for consequent ecological research (Ball, 1979, 1996; Stork, 1988; Stork, 1994; Samways, 1994). However, because of the handsome elegant appearance displayed by many of the more noticeable species (Hammond, 1990), carabids have been intensively studied by generations of Coleopterists and they are currently one of the best known invertebrate families (Desender *et al.*, 1994). This knowledge has been accumulated from studies mostly based in the northern hemisphere where evolutionary and ecological hypotheses have been tested (Lindroth, 1949; Den Boer, 1986; Loreau, 1994). More recently, carabids have been used for more applied studies, such as conservation and evaluation (Stork, 1990; Luff and Woiwod, 1995; Desender *et al.*, 1994; Thacker, 1996; Niemela, 1996a, 1997). Specifically, carabids have been used as indicator organisms for assessments of environmental pollution (Heliovaara and Vaisanen, 1993), habitat classification for nature protection (Luff, *et al.*, 1992; Pizzolotto, 1994; Eversham *et al.*, 1996; Eyre, *et al.*, 1996; Luff, 1996), or characterization of soil nutrient status in forestry (Szyszko, 1983). They might also serve as biodiversity indicators.

Eyre *et al.* (1996) have shown that there is great potential for the use of ground beetle data obtained from structured and standardized surveys for environmental monitoring. Their methodology has

worked at the local, regional and national scales. There is much carabid information in Europe (Eyre and Luff, 1990a; Turin *et al.*, 1991; Maelfait *et al.*, 1994), and Eyre *et al.* (1996), suggest that, it can provide a basis for very large-scale work and has the potential for an integrated approach covering a number of countries. Currently, there is no ground beetle ecological information in southern Africa. This study therefore aims to start documenting such information which can then be integrated with that of the northern hemisphere.

Another advantage of carabids is that they can be fairly reliably and quantitatively collected by pitfall traps (Luff, 1975; 1996; Spence and Niemela, 1994, Digweed *et al.*, 1995). Even the majority of studies presented at the 3rd International Symposium of Carabidology were based on pitfall trapping, and about 75% of them dealt with questions related to the effects of human activities on carabids or on the use of carabids in conservation studies. The increase of these studies is very encouraging, as invertebrates have been rarely used in conservation studies, although their potential is immense (Wilson, 1987; Franklin, 1993; Kim, 1993; Kremen *et al.*, 1993; Miller, 1993).

Considerable controversy surrounds the classification of tiger beetles as a group within the suborder Adephaga. Various authors have placed them as a subfamily (Cicindelinae), tribe (Cicindelini), or supertribe (Cicindelitae) within the family Carabidae (Ball, 1979). Others have placed them in their own family Cicindelidae (Nichols, 1985; Scholtz and Holm, 1986). Although this placement is used in this study, both Carabidae and Cicindelidae are considered here.

The last attempted synthesis on carabid biology was by Thiele (1977). Only certain aspects of the field have been reviewed since (Allen, 1979; Laroche, 1990; Luff, 1987; Niemela, 1993b). More recently, Stork (1990), Niemela (1996,1997), and Lovei and Sunderland (1996) have summarized some of the significant achievements in carabid ecology.

Although carabids are worldwide, with species richness highest in the tropical regions (Darlington, 1943; Erwin, 1985; Ball, 1985; Noonan *et al.*, 1992), the current available knowledge stems from research done in the temperate regions of the northern hemisphere, with little having been done in the south. A major aim of this study is to report on some initial findings that will contribute towards filling this gap in knowledge, by looking at aspects of carabid ecology, such as monitoring their

response to landscape disturbances and seasonal variations in the southern hemisphere.

1.4.1 Landscape disturbances and body size distribution of carabid beetles

Patterns of body size distributions are of great ecological interest, and there is much literature dealing with the relationships between body size and community structure both in general and for arthropods, Coleoptera in particular (Van Valen, 1973; Peters and Wassenberg, 1983; Tietze, 1985; Sustek, 1987; Morse *et al.*, 1988; Maurer and Brown, 1988; Gaston and Lawton, 1988; Lawton, 1990; Blackburn *et al.*, 1990; Loreau, 1992; Stork and Blackburn, 1993; Eyre, 1994; Blake *et al.*, 1994). Apart from the work of Blake *et al.* (1994), there is little quantitative information, on how the average body size of carabid assemblages varies between or within different habitats. In a few studies, larger species were found to be more abundant in less disturbed habitats (Tietze, 1985; Sustek, 1987; Eyre, 1994; Blake *et al.*, 1994).

Sustek (1987) found that disturbance by urbanisation displaced the carabid body size distribution curve towards smaller size. Tietze (1985) found that after ten years of intensified management of a grassland in Russia, carabid diversity overall had decreased, with large species being especially affected. Eyre and Luff (1990b) analysed pitfall data from 363 British grassland sites, and found intensity of management an important factor affecting species assemblage distribution. Blake *et al.* (1994) assessed pitfall data from 50 grassland, nine moorland and 39 woodland sites, and concluded that disturbed habitats support a carabid fauna of smaller average body size. They discussed some possible reasons for this and its implications for conservation, especially of wading birds and other species preying on carabids.

This study aims to determine effects of habitat type and management practices on body size distribution of carabid beetles living in the southern hemisphere, and to compare these findings with those of the northern hemisphere.

1.5 AIMS OF THIS STUDY

The 400m escarpment near the city of Pietermaritzburg, South Africa, has led to the creation of a great variety of landscape types, including different natural and planted forests, nature reserves and

various types of agricultural land. Each of these landscapes is exposed to a particular type of disturbance, both regular and irregular. Such disturbances include management practices such as mowing, irrigation, fires, tree felling, fertilizers and pesticides. In other words, there is great variation in biotope and landscape type without invoking regional differences.

The aims of the study are to use carabids and cicindelids at the species level to determine their responses to prescribed fire management and mowing disturbances in grasslands of road verges, parks and hayfields; to determine whether road verges in the southern hemisphere have high potential for conservation value as has been proposed by Eversham *et al.* (1996) in the northern hemisphere; to determine the responses of species in this region of the southern hemisphere to forest management and to identify which species are most vulnerable; to monitor the response of carabids and cicindelids to agricultural management disturbances in a macadamia orchard so that management for biodiversity can be put in place; to determine the use of carabids and cicindelids as biodiversity indicators and their use in monitoring programmes to detect effects of management and refine it as needed; to determine effects of habitat type and management practices on body size distribution of carabid beetles living in the southern hemisphere, and to compare these findings with those of the northern hemisphere; to start documenting carabid ecology information in the southern hemisphere such as spatial patterns and seasonal variations which can then be integrated with that of the northern hemisphere.

The macroecological approach was used as a management tool to distinguish between the local effects of disturbance in the southern hemisphere and the general global effects. The null hypothesis was that there are no differences in the distribution patterns of carabids and cicindelids in various types and intensities of landscape disturbance at the local and global scale. Against this background, the following questions were addressed:

- 1) What are the carabid and cicindelid point distributions for various types and intensities of landscape disturbance, both human and natural?
- 2) Which single species and/or assemblages are good indicators of these disturbances?
- 3) Which species can, and which cannot, survive particular disturbances?

- 4) Can the pitfall captures of these animals be used to characterize the various landscape types and disturbances?
- 5) Can pitfall captures of these animals be used to monitor and evaluate temporal changes at a given site?
- 6) Which species can be used for making management recommendations and improve the conservation of landscapes?
- 7) How do these local distribution patterns and responses compare with other parts of the world?

CHAPTER 2

SITES

2.1 INTRODUCTION

The study area was an altitudinal-gradient transect running across two distinct geographical zones, namely Escarpment and Savanna, situated 20 km apart (Fig. 2.1a and Fig.2.1b). The Escarpment Zone has an altitude range of 850 metres to 1140 metres above sea level. The Savanna Zone ranges from 700 metres to 830 metres above sea level. Even though the two regions were only 20 km apart, they had distinct climates and vegetation types. This made it possible for the study to be carried out in two distinct zones, each with four clear landscape elements (sites) over the same period of time (June 1994-May 1996). The aim was to maximize habitat heterogeneity in order to determine carabid and cicindelid distribution patterns on a small scale (in the range of a few metres within landscapes); the local scale (patterns across landscapes), and thirdly, at the biogeographical scale (Niemela, 1997). Fig. 2.1(a) and (b) shows that samples were collected over a range of eight landscape elements from which four point habitats were sampled from each landscape giving a total of 32 point habitats (but 128 traps) over the whole study area. See details of the sampling methods in Chapter 3.

The sites were selected for study with the law of parsimony prevailing. Questions like how many traps could one handle in maximizing habitat heterogeneity and get maximum information on phenology and at the same time stay within the limits of a tight budget were considered. As a result this initial study was limited to an altitude of 900 metres above sea level within the Escarpment Zone and 700 metres above sea level within the Savanna Zone. This study area still provided maximum differences in the smallest space.

Table 2.1 is a summary describing the various landscape types and disturbances. A detailed geographical description of the Escarpment and Savanna Zones (situation, topography, history, geology, climate, hydrology, vegetation and fauna) now follows.

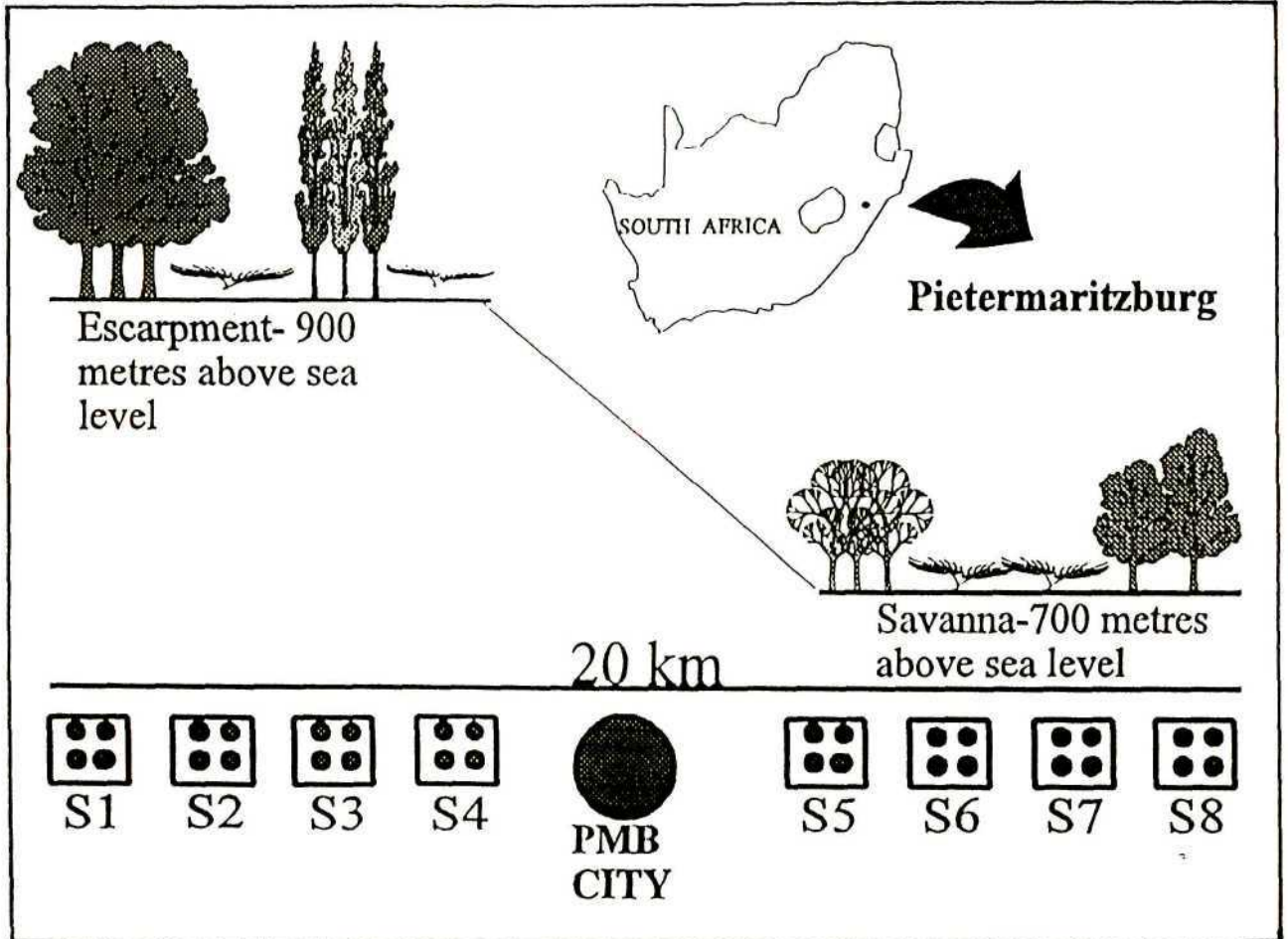


Figure 2.1(a): An altitudinal-gradient transect running across two distinct geographical zones (Escarpment and Savanna) situated 20 kilometres apart in the vicinity of Pietermaritzburg city, South Africa. The transect runs through four grassland and four forest landscape elements (sites S1-S8), with each landscape element (site) consisting of four point habitats shown as dots. Point habitats were situated at various distances apart (10 metres to about 500 metres) within and among sites. Each point habitat was sampled with four pitfall traps. For further sampling details, see Chapter 3.

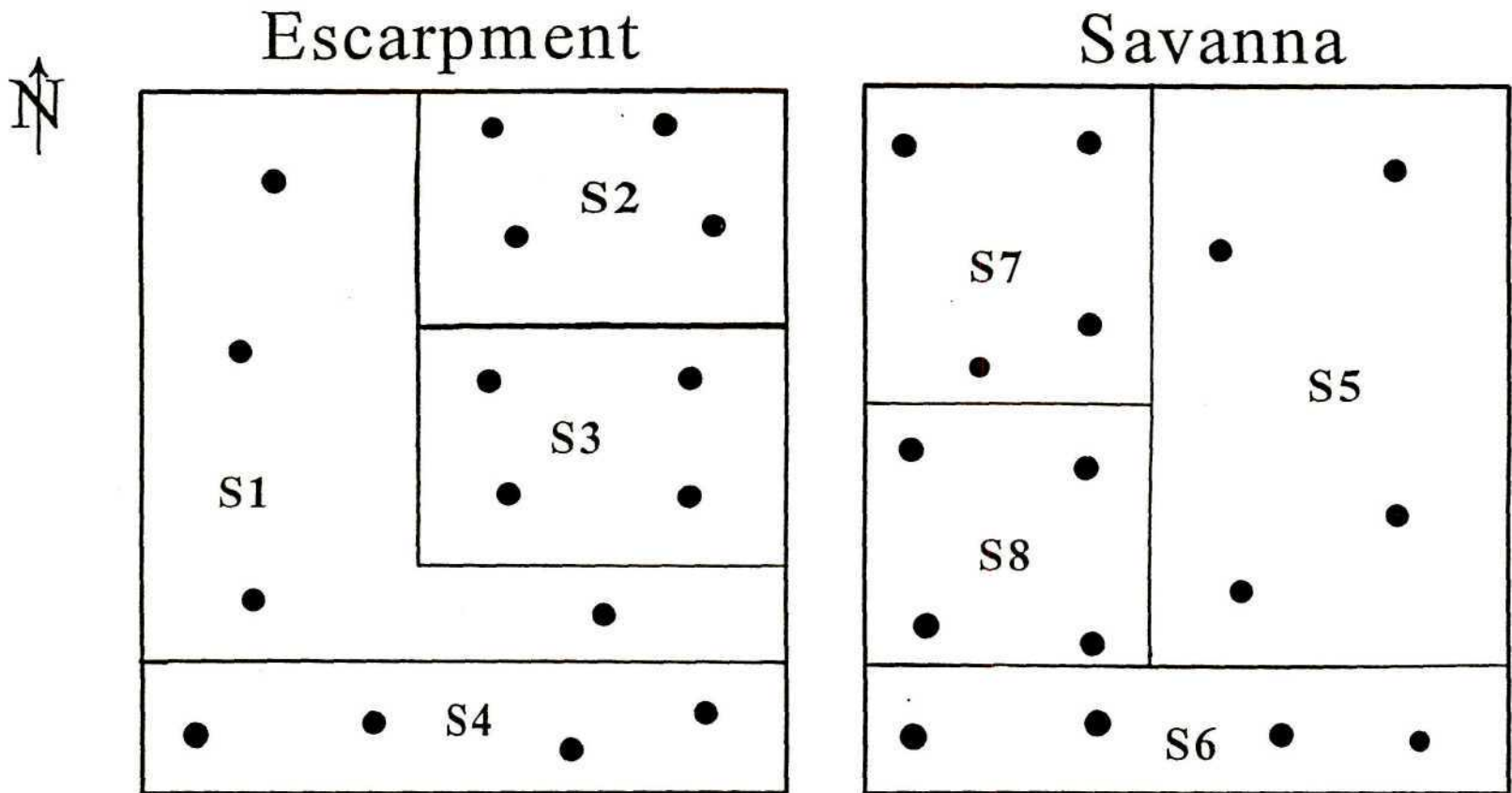


Figure 2.1(b): Schematic map of the study area showing the position of the different landscape elements (sites) relative to each other in the Escarpment and Savanna Zones, namely, mistbelt *Podocarpus* forest under nature management (S1), pine plantation (S2), a park (S3), road verge grasslands (S4) and (S6), *Acacia*-dominated woodland under nature management (S5), a grassland field (S8). The dots are four point habitats sampled per each of the eight sites. Each point habitat was sampled with four pitfall traps. For further sampling details, see Chapter 3.

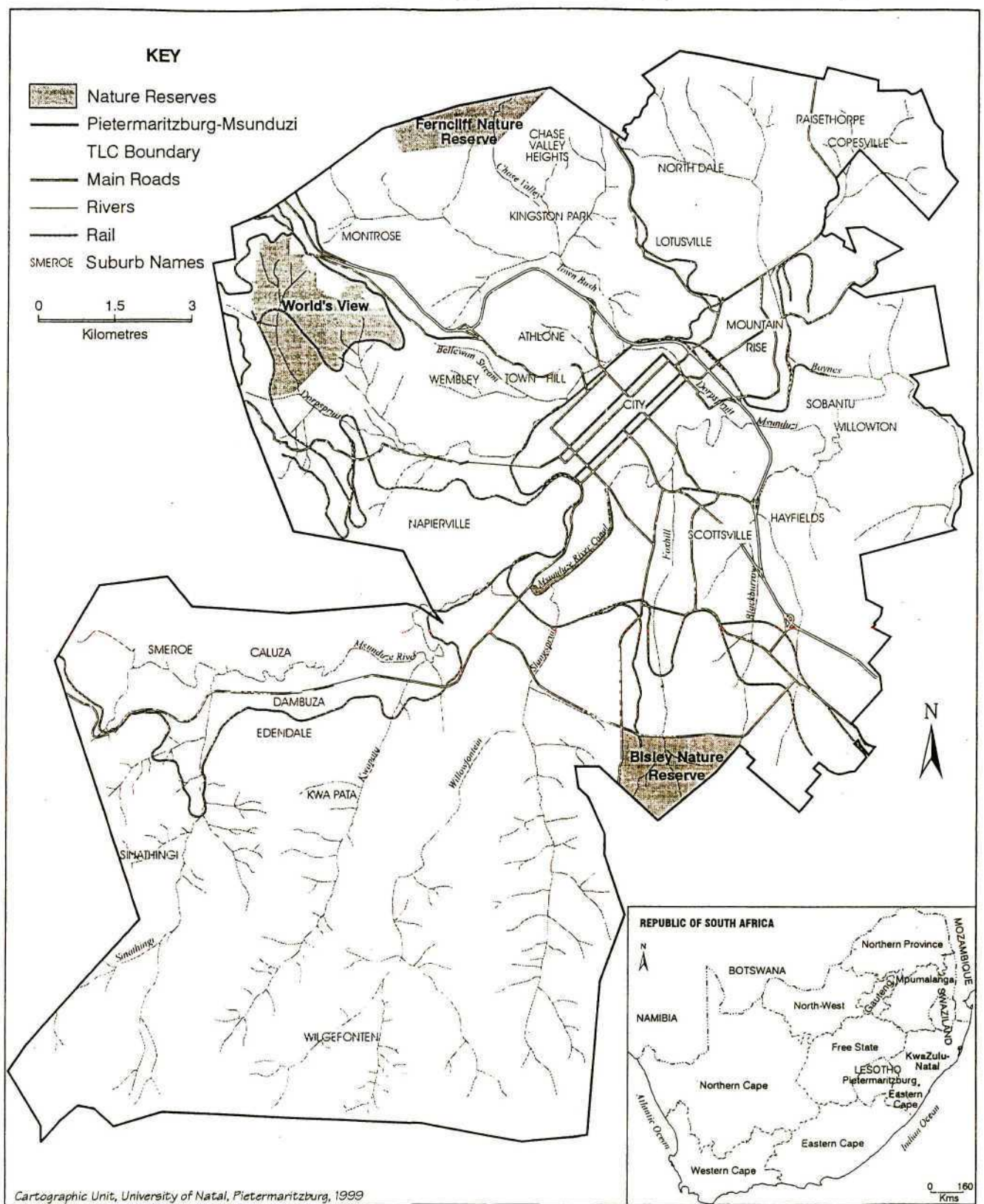


Figure 2.1(c): Actual map of the localities of study sites (three nature reserves) as Ferncliffe nature reserve, World's view nature reserve and Bisley nature reserve

SITE	LANDSCAPE ELEMENTS (HABITAT TYPES)	TYPE OF DISTURBANCE OR LANDUSE AND ITS ABBREVIATIONS	ELEVATION (m.a.s.l.) High = 900 Low = 700	POINT HABITATS	LOCATION
1	A mistbelt mixed <i>Podocarpus</i> forest (primary natural forest)	Nature management (NM)	High (escarpment)	1-4	Ferncliffe Nature Reserve
2	A pine plantation (<i>Pinus patula</i> Schiede ex Schlecht. et Cham) (secondary forest)	Planted managed forest pruned once in August of first sampling season (PP)	High (escarpment)	5-8	Ferncliffe Nature Reserve
3	A recreational park grassland	Park lawn kept short and mown (PA)	High (escarpment)	9-12	Ferncliffe Nature Reserve
4	A road verge grassland	Road verge under management of autumn (May/June) burning in the first sampling season and grass cut along a strip of five metres wide under electricity posts as a maintenance routine in the second season (RV)	High (escarpment)	13-16	World's View
5	<i>Acacia</i> -dominated thornveld woodland (primary natural forest)	Nature management (NM)	Low (savanna)	17-20	Bisley Nature Reserve
6	A road verge grassland	Management of autumn burning (RV)	Low (savanna)	21-24	Bisley Nature Reserve
7	A macadamia plantation (secondary forest)	Agricultural management - irrigation, fertilizers, pesticides, pruning (MP)	Low (savanna)	25-28	Ukulinga Research Farm
8	A grassland field	Field with grass harvested for hay once a year (FD)	Low (savanna)	29-32	Ukulinga Research Farm

Table 2.1: A summary of the eight landscape elements (sites) used in this study, with their abbreviations pertaining to type of disturbance or landuse. Four point habitats per landscape element were sampled. Further details can be found in the text, (Chapter 3, Section 3.3.4). Metres above sea level (m.a.s.l.).

2.2 FERNCLIFFE NATURE RESERVE

2.2.1 Situation and topography

Ferncliffe Nature Reserve (250 ha) is situated at about 29° 33'S 30° 20'E. It is elongated in a WSW-ENE direction with the upper boundary being the top of the Escarpment (Municipal boundary) and the lower boundary being the "forest contour road". The longest dimension is 19 approximately 4.2 kilometres and the average width approximately 600 metres. The highest point is at 1140 metres above sea level and the lowest point is at 850 metres. The relief is therefore 290 metres.

2.2.2 History

The land was acquired in the mid 1850's by Jesse Smith a stonemason from England. He drilled, blasted and dressed sandstone on the Escarpment for commercial use. Quarrying of the stone at Ferncliffe continued until 1938 when it was sold to the City Council. In 1954 the Council approved an afforestation and plantation programme and grasslands surrounding the indigenous forest were planted to pine and gum.

Today the forestry areas are administered and maintained by Natal Co-operative Timbers and the Conservation section of the Parks and Recreation Department of the city of Pietermaritzburg are responsible for the maintenance and development of the indigenous forest areas.

2.2.3 Geology

Gritty and often friable sandstone forms the top of the indented Escarpment running through the Kwazulu-Natal Midlands just west of the line joining Greytown, Pietermaritzburg and Ixopo. The sandstone and beds of shale on Ferncliffe are components of the Middle Ecca Series. The early horizontal beds are laid down in a large freshwater lake about 200 million years ago (Nanni, Undated).

The following soil forms have been identified in the area: Avalon, Bainsvlei, Clovelly, Griffin, Hutton, Inanda, Katspruit, Westleigh, Mispah (Soil classification, 1991).

Soil depths range from <300 mm to >1000 mm (Anonymous, 1990). The A horizons are more

stable and thus more suitable for path treads given suitable protection from high velocity surface run-off. If the A horizon is removed by accelerated erosion, in areas other than footpaths, expensive rehabilitation will be required to re-establish a plant cover. In general, the dense natural forest keeps erosion to a minimum and the major erosion of the area is through landslides, (Nanni, Undated).

The soils are well drained, highly leached, acidic and have a low nutrient content (Anonymous, 1990). These soils are typical of high rainfall, low mean temperature areas.

2.2.4 Climate

Ferncliffe has a summer rainfall. Approximately 80% of the rain falls during the months of October to March inclusive. The wettest months are around midsummer i.e December, January and February. The driest months are over winter i.e. June and July. The average annual rainfall is estimated to be 1100 mm.

Average daily sunshine varies from 7.5 hours during summer to approximately 5.5 hours in winter. Due to the rapidly rising Escarpment at Ferncliffe the sun sets approximately 2 hours earlier in winter than on areas further from the Escarpment. The above and the high incidence of mist days during summer account for the relatively low sunshine hours.

The prevailing summer winds are light and usually from the east. Summer thunderstorms may be accompanied by strong winds usually from the south or west. Late winter winds originate in the north-west or west. These desiccating winds do not seriously affect the vegetation as Ferncliffe lies on sheltered south facing slopes.

2.2.5 Hydrology

The drainage lines in the Ferncliffe area are in a roughly north-south direction. The headwaters of two streams are formed in the area, namely Chase Valley stream and Town Bush stream. These streams are tributaries of the Dorpspruit (a small river) which in turn flows into the Umsinduzi river. The Ferncliffe Escarpment thus plays an important role, with its high rainfall, in the production of a sustained yield of water for the Umsinduzi system.

2.2.6 Vegetation

2.2.6.1 A natural indigenous primary forest (Site 1)

The Ferncliffe area contains cool, tall, inland moist high forest known as Mist Belt Ngongoni Veld (Acocks, 1975) or Mistbelt Mixed *Podocarpus* forest (Edwards, 1967; Pooley, 1993) under nature management (Fig.2.2).

These forests are famous for fine specimens of yellow-woods, with *Podocarpus falcatus* (Thunb.) being generally the most common together with a rich mix of other species including endemics (Pooley, 1993). Due to past management practices, exploitation and the encroachment of invader plants, the forest is now in a poor state of preservation. Many indigenous species occur in the area.

2.2.6.2 A pine plantation forest (Site 2)

An afforestation and plantation programme approved by the City Council and run by Natal Cooperative Timbers has been in operation since 1954 and grasslands surrounding the indigenous forest have been planted with pine and gum. The forest stand under study was stand A28 of pine (*Pinus patula* Schiede ex Schlecht. et Cham) covering an area of about one hectare but bordered by other more mature stands of pine on either side separated by a road and a recreational park on the other side. The pine plantation studied is about 200 metres from the natural indigenous forest (S1) (Fig.2.1 and Fig.2.3). The stand was planted in 1984 and insect sampling for this study was carried out between June 1994 to May 1996 when the trees were aged 10-12 years. The nature of disturbance was pruning which took place during August of 1994. This was the second pruning at five metres height of trees. The first pruning had taken place at three metres height. The amount of shade cover decreased and herb cover increased. Therefore the stand under study was in the medium regeneration stage. Trees are usually felled at the age of 20-25 years and sometimes at the age 30 years.

2.2.6.3 A road verge grassland (Site 4)

A road verge ranging from approximately 20 metres to 100 metres wide over one half of a kilometre dominated by the grass species *Aristida junciformis* (Trin. & Rupr.) SSP. *junciformis*

“Ngongoni” that grows to a maximum height of about 67 cm, (Tainton *et al.*, 1976). Other less dominant grass species were *Panicum natalense* (Hochst.), *Monocymbium ceresiiforme* (Nees.) “wild oat grass”, *Themeda triandra* (Forssk.) “Redgrass”. The road verge is a grassland with intensive management of burning once a year during autumn (May/June) as a City Council management strategy of ensuring fresh green growth of grass and prevention of accidental fires and bush encroachment. Grass is also cut along a narrow strip of five metres wide under electricity posts as a maintenance routine (Fig.2.4).

2.2.6.4 A recreational park grassland (Site 3)

A park recreational site approximately one hectare in extent bordered by a natural indigenous forest on one side and pine plantation forest on the other side. The park was dominated by lawn grass *Axonopus affinis* (Chase) “carpet grass” and was kept mown at least over six times in a year and it has three areas with stones for landscaping in which ornamental flowers are grown. It has individual indigenous trees spaced within it and guava and lemon trees (Fig.2.5 and Fig.2.1).

2.2.7 Fauna

The present large mammal population is restricted mainly to forest-dwelling species. No comprehensive sighting records are available for the area but the following species have been sighted since April 1990: vervet monkey (*Cercopithecus aethiops*), porcupine (*Hystrix africae australis*), bushbuck (*Tragelaphus scriptus*), blue duiker (*Philantomba monticola*), (Nanni, undated). The blue duiker (*Philantomba monticola*) is listed as rare in the South African Red Data Book (Smithers, 1986).

The Ferncliffe area supports a large and varied population of birds, particularly forest and forest-margin species. There are no records of the invertebrate fauna at Ferncliffe and this study is therefore intended to fill in part, this missing gap. Many of the indigenous plants in the area are dependent on forest animals for seed dispersal and indirectly on the invertebrate fauna. Management objectives should be aimed at the re-habilitation and maintenance of habitat. A natural consequence of this action is the conservation of fauna utilising these habitats.

2.3 BISLEY NATURE RESERVE

2.3.1 Situation and topography

Bisley valley nature reserve is approximately 250 hectares in extent. The reserve is bordered by the Richmond road in the west, Murray road in the North and the Natal University Research Farm, Ukulinga, in the south and east. The highest point of the property is at 830 metres above sea level and the lowest point is at 700 metres a.s.l. The relief is therefore 130 metres.

2.3.2 History

Bisley Valley has a long association with rifle practice. The area was used for this purpose by the British Garrison at Fort Napier until their departure in 1913. Shooting practice in the area continued into the early 1900's with the annual Bisley competition and two further butts or ranges were built during World War II. Evidence of early iron age settlements have been found and this indicates the first intensive use of the area. It has also been used for grazing by lessee farmers and a horse riding school still occupies a portion of the reserve.

2.3.3 Geology

The following soil forms have been identified: Mispah, Clovely, Avalon, Westleigh, Bonheim, Valsrivier, Glenrosa, Swartland, Inhoek, Katspruit, and Dundee. Soil depths range from 300 mm to 1000 mm (Anonymous, 1990). Rock outcrops are predominantly dolerite, with some shale outcrops particularly in the lower lying riverine areas.

2.3.4 Climate

Bisley nature reserve, unlike Ferncliffe nature reserve, is hot and dry and subject to considerably less rainfall. The area lies within the summer rainfall regions of southern Africa with an annual mean of 705.5 mm. the mean annual temperature is 18.2^o C with a range of between 12.9^o C and 23.6^o C.

2.3.5 Hydrology

The Foxhill Spruit (a stream) originates just south of Bisley valley and effectively bisects the

reserve in addition two tributaries of the Foxhill Spruit originate within the reserve one of which is fed by a wetland. Approximately 7.5 kilometres from its confluence the Foxhill Spruit flows into the Umsinduzi River. Under normal conditions the Foxhill Spruit is dry in winter but the tributary fed by the wetland appears to be perennial. The management of the reserve therefore has a direct impact on the sustained flow of water in the Foxhill Spruit.

2.3.6 Vegetation

2.3.6.1 *Acacia-dominated thornveld as a primary natural woodland (Site 5)*

The vegetation of Bisley Valley falls into the southern tall grassveld described by (Acocks, 1975). He describes tall grassveld as "An open Savanna of *Acacia sieberana* var. *woodii* (Burt Davy) in sourish mixed grassveld with plentiful patches of *Hyparrhenia hirta* (L.) Stapf. and other species of *Hyparrhenia*. Soils resemble those of the dohne sourveld in having an erodible subsoil, but the top soil is much shallower (300 mm-450 mm) so that erosion is severe in this veld type. *Themeda* and *Hyparrhenia* grasses are most abundant on dolerite, and most of the outliers of the southern tall grassveld are on dolerite. There are indications that the natural vegetation of the flat, exposed parts of this veld type may have been scrub forest".

The vegetation can be divided into four distinct habitat types namely low open woodland, low closed woodland, short riverine thicket and wetland (Hurt, 1987). The riverine thicket occurs on deep soils along the watercourses and is characterised by a dense, impenetrable structure dominated by *Acacia karroo* (Hayne), *Acacia ataxacantha* (DC.), *Rhus* sp. and *Buddleja saligna* (Willd.). The low open woodland and low closed woodland are found on shallower soils away from the watercourses. The low closed woodland was severely infested with *Lantana camara* with mature specimens of *Acacia sieberana* (Burt Davy), usually an open woodland species, surrounded by *Acacia nilotica* (L.) and *Acacia karroo* (Hayne), which are predominantly closed woodland species. This would appear to indicate that infrequent burns and the encroachment of *L. camara* (an exotic species) have resulted in a change from open woodland to closed woodland in parts of the reserve (Hurt, 1986).

A generalised description of the vegetation in this site would be 'Acacia-dominated thornveld'. Fig. 2.1 and Fig. 2.6 shows the landscape labelled as site 5.

2.3.6.2 A road verge grassland (Site 6)

A road verge grassland approximately 30 metres wide dominated by *Hyparrhenia* grass species that grows to a maximum height of about 67 cm, (Tainton *et al.*, 1976). The road verge is a grassland with intensive management of burning once a year during autumn (May/June) as a city council management strategy of ensuring fresh green growth of grass and prevention of accidental fires and encroachment of bush. See Fig.2.6.

2.3.7 Fauna

Due to the diversity of habitats encountered in Bisley, there is a great faunal diversity, especially of birds (161) species (Maclean, 1993). In addition, the reserve has been identified as a suitable oribi (*Ourebia ourebi* Zimmermann) habitat. The oribi is a rare animal listed as 'Vulnerable' in the South African Red Data Book (Smithers, 1986).

The invertebrate fauna at Bisley has not been recorded. This study is intended to fill in part of this missing gap. The conservation and correct management of Bisley Nature Reserve is vitally important for the preservation of these species in the area.

2.4 UKULINGA RESEARCH FARM

2.4.1 Situation and topography

Ukulinga farm (29° 40' 15"S 30° 24' 28"E and an altitude of 775 metres) borders Bisley Nature Reserve and the two are similar geographically with a Savanna climate. Therefore annual mean rainfall and temperature is the same as that of Bisley, see Section 2.3.

2.4.2 Vegetation

2.4.2.1 A macadamia plantation (orchard) (Site 7)

The macadamia or Queensland nut, *Macadamia ternifolia* F. Muell. (Proteaceae), originated in eastern Australia. It is grown on a small scale in the frost-free parts of South Africa, the northern and eastern lowveld and along the Kwazulu-Natal coast where avocados, bananas and granadillas flourish. The insect pests recorded on macadamia so far are armoured scales,

aphids, coconut bugs, stinkbugs, thrips, moths, caterpillars and bark borers (Annecke and Moran, 1982).

The macadamia plantation (orchard) is one hectare in extent, with various plant cultivars. Intensive irrigation by means of micro sprinklers is carried out throughout the year. Each tree is applied with a total of the following fertilizers per year: LAN(4.5 kg); KCL(1.4 kg); Solubor (three times a year as Boron trace element); SSP(2.5 kg) and Lime(4 kg). Fertilizer applications are done at the end of October and April of every year. Insecticide (Cypermethrin) application is carried out two times in a year in November and January mainly for stinkbug control. The nuts are harvested between May and July with the main harvest appearing in June. See Fig 2.7 and Fig.2.1.

Adjacent to the macadamia plantation forest is a one hectare plantation of citrus on one side, a *Eucalyptus* hedge on the other and a grassland field as site 8 below.

2.4.2.2 A grassland field (Site 8)

This is grassland which is one hectare in extent and borders the macadamia plantation. The grass grows to a maximum height of about 144 cm (Tainton *et al.*, 1976) and is harvested for hay once a year in May/June. The grassland is dominated by the grass species *Panicum maximum* (Jacq.) known as “guinea grass” and to a lesser degree by *Rhynchetlyrum repens* (willd.) “Natal red top” (Fig.2.8 and Fig.2.1).



Figure 2.2: Site 1-A mistbelt mixed *Podocarpus* forest, a primary natural forest with many indigenous tree species under nature management. It is situated in the Escarpment Zone at high elevation



Figure 2.3: Site 2-Pine plantation (*Pinus patula*) in the mid-successional stage, an introduced secondary forest pruned once in August during the first sampling season. It is situated in the Escarpment Zone at high elevation

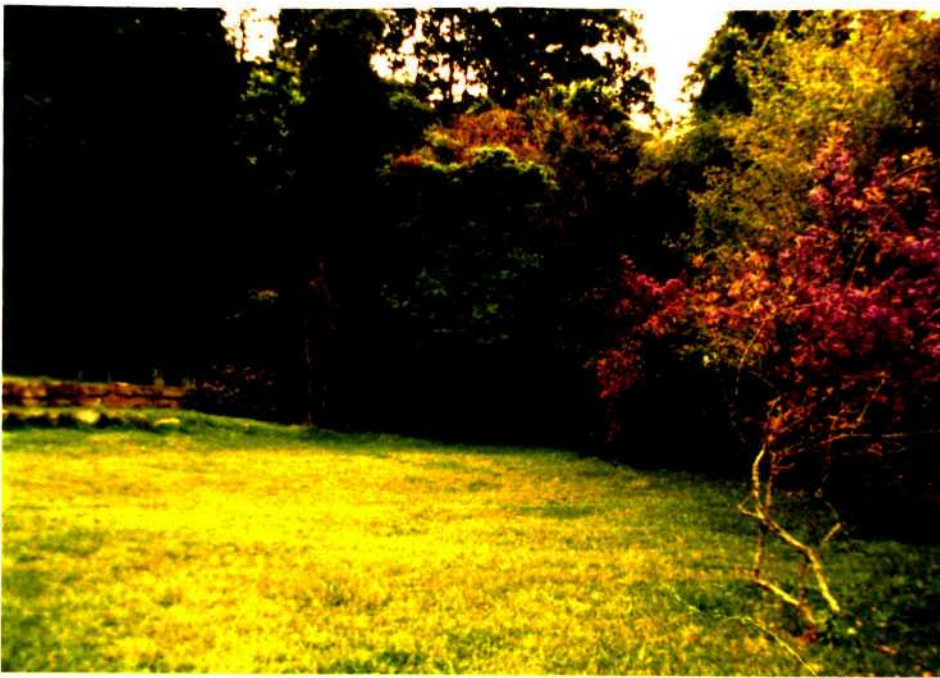


Figure 2.4: Site 3-A recreational park grassland with a lawn kept mown throughout the year but having some indigenous tree species in addition to lemon and guava trees and ornamental flowers. It is situated in the Escarpment Zone at high elevation.

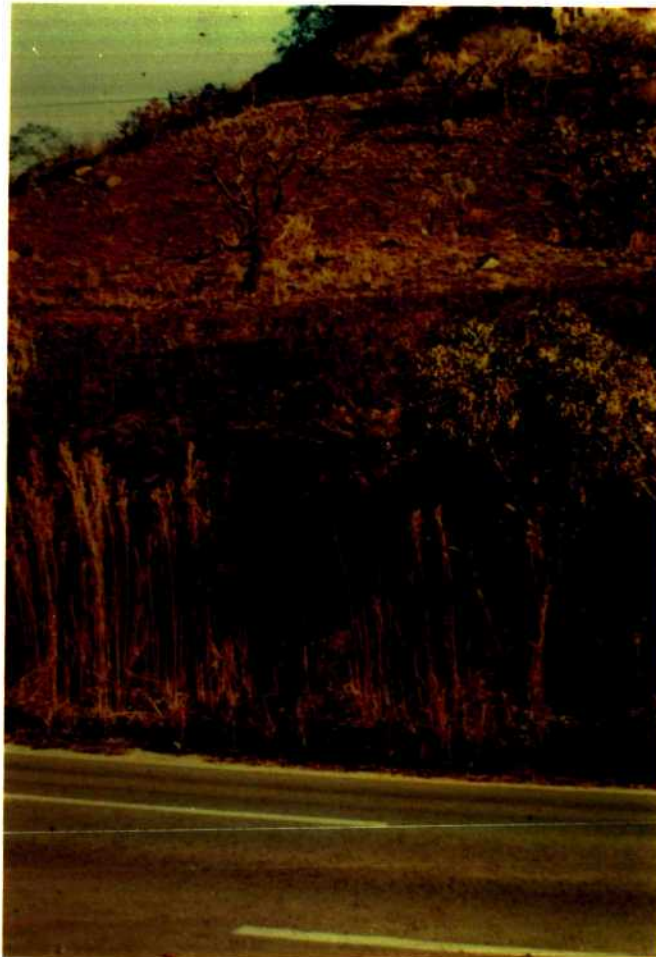


Figure 2.5: Site 4-A road verge grassland with autumn burning as a City Council management strategy of preventing accidental fires and bush encroachment. Grass is also cut along a narrow strip of 5 metres wide under electricity posts as a maintenance routine. It is situated in the Escarpment Zone at high elevation.



Figure 2.6: Site 5-*Acacia*-dominated thornveld woodland, a primary natural forest under nature management and Site 6 is a road verge grassland under autumn burning management situated in the same Savanna Zone at lower elevation



Figure 2.7: Site 7-A macadamia plantation (orchard) under agricultural management-irrigation, fertilizers, pesticides, pruning situated in the Savanna Zone at lower elevation



Figure 2.8: Site 8-A grassland field with grass mown once a year bordering macadamia plantation situated in the Savanna Zone at lower elevation

CHAPTER 3

MATERIALS AND METHODS

3.1 INTRODUCTION

Pitfall trapping has been one of the most used methods for sampling assemblages of ground-dwelling arthropods. The method is popular because it is convenient, inexpensive and labour-efficient and allows collection of arthropods in numbers suitable for rigorous statistical analysis (Spence and Niemela-1994).

Pitfall samples have been used successfully as population indices for comparison of carabid activity between years or across similar habitats. However, pitfall data must be viewed cautiously if used to provide comparative estimates of species abundance across habitats (Mitchell, 1963; Greenslade, 1964; Niemela *et al.*, 1990) because it has been reported that, even though pitfall catches reflect activity and density of the animals (Trezel, 1955; Thiele, 1977; Luff, 1982 1986; Franke *et al.*, 1988), they are also influenced by other factors such as temperature and moisture (Ericson, 1979; Honek, 1988), surrounding vegetation (Greenslade, 1964), materials used for the construction of the trap (Luff, 1975), preservative (Wagge, 1985), number, size, shape and arrangement of traps (Orbtel, 1971; Adis, 1979; Niemela *et al.*, 1986b), biology of the species like seasonal activity rhythms and behaviour (Spence and Niemela, 1994; Luff, 1996).

It is therefore important to tailor a sampling programme to the species and habitats with which one works and interpret the data obtained from a sounder base of biological intuition. The choice of a sampling method depends on the questions to be studied. In surveys of large geographical areas where the objective is qualitative inventory and comparison of assemblages, pitfall trapping is the only realistic alternative presently available (Van den Berghe, 1992; Niemela *et al.*, 1990, 1993; Niemela, 1996b; Sunderland *et al.*, 1996). The kind of work may involve assessing and monitoring environmental problems by using carabids as an 'indicator' group (Freitag *et al.*, 1973; Niemela *et al.*, 1990; Luff, 1996).

This study was carried out to determine the carabid and cicindelid point distributions relative to four forest and four grassland habitats along an altitude-gradient transect across two geographical zones and also to determine the distribution patterns across two seasons or two years. In this study the following sampling programme using pitfall traps, window traps and visual searching were carried out.

3.2 MATERIALS

3.2.1 Pitfall Traps

The pitfall trap Fig.3.1 (a) and (b) was a modification of the type used by Van den Berghe (1992) and Spence and Niemela (1994). Traps consisted of an inner round plastic drink cup that can be found in most stores. The plastic material was 1.43 mm thick with a 7.5 cm mouth diameter and 7.6 cm deep with a capacity of 240 ml.

It was found that cups with a smaller thickness of 0.35 mm and less, like yoghurt containers became too brittle and easily cracked after periods of 2-3 months in the hot Savanna areas and 5-6 months in the cooler Escarpment Zone and were therefore found not to be suitable for use over the two year sampling period.

It was also found that two-month trial runs using one litre yoghurt cups with a 12.0 cm mouth diameter and 12.7 cm deep, required more collecting fluid (200 ml instead of 100 ml) causing an unnecessary extra expense and weight. The one litre cups trapped more small vertebrates like frogs, mice and lizards when compared with the smaller 240 ml cups. This interfered with the trapping efficiency for invertebrates as small vertebrates easily escaped from the 240 ml cups than the 1000 ml cups. The smaller cups were also easier and faster to install.

3.2.2 Pitfall trap modifications

Eight holes, each 1 mm in diameter, were placed at equal distances around the 240 ml cups to prevent the problem of traps filling with water after heavy rains and spilling out specimens. The first row of 4 holes was at 4.5 cm level from the bottom. The second row of another 4 holes was placed at 7.0 cm level from the bottom in alternating positions with the first row. A tool used by shoe repairers to punch holes through leather was used.

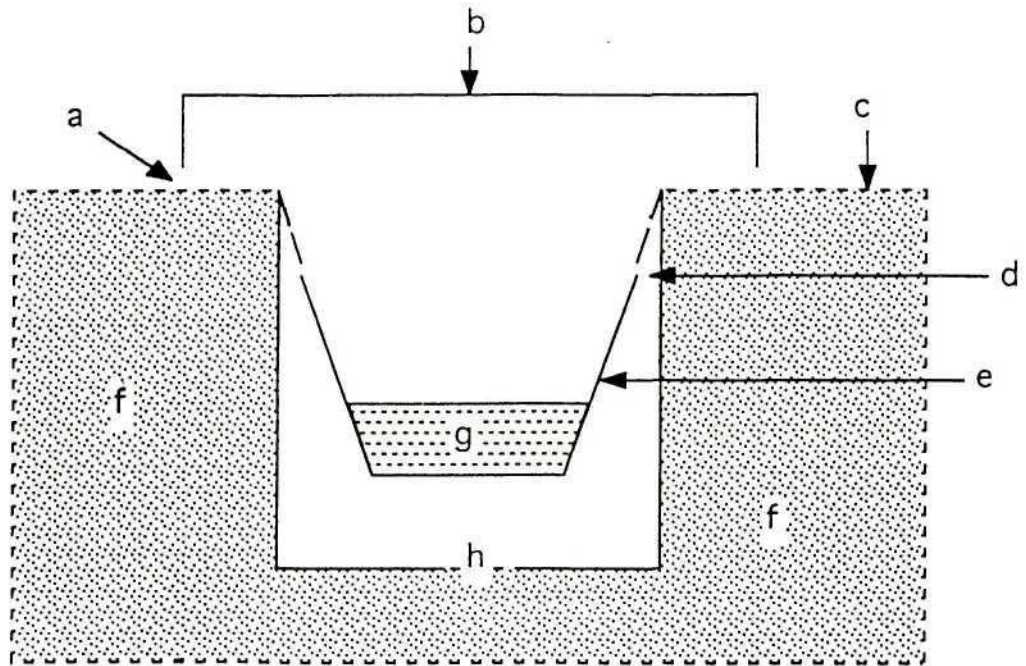


Figure 3.1(a): Cross-section through a pitfall trap. (a)-Opening into trap, (b)- PVC roof 15 cm by 11 cm by 7 cm , with openings into trap from four sides, (c)-Ground level, (d)-Holes in the trap 1 mm in diameter to let out flood water, (e)-An inner trap as a plastic drink cup with a mouth diameter of 7.5 cm and 240 ml capacity, (f)-Earth, (g)-Collecting fluid as one part ethylene glycol and one part water, (h)-Outer jar as a plastic container inserted into the earth to hold the inner cup. It has a hole at the bottom to let out any flood water that overflows from the inner cup.



Figure 3.1(b): The three components that make up the pitfall trap. From left to right is the plastic drink cup that makes up the inner trap; a plastic jar that makes the outer container which holds the inner trap; PVC guttering cut in a table shape and used as a roof over the trap.

When emptying trap contents, it was found that continued removal and re-sinking of traps disturbed the surroundings in addition to being tedious and labour intensive. Hand operated or mechanical suction apparatus for emptying traps could not be operated successfully because traps tended to collect leaves, debris and soil during windy heavy rains which made it impossible to see all specimens caught. And as the highest beetle activity coincided with the rainy summer months, there was a high risk of losing specimens caught in the traps as it was not possible to see clearly through muddy flood waters in the traps after heavy rains. The idea of sorting specimens in the field was therefore not possible as they became covered in soil and leaves and were not seen. In order to facilitate emptying, an outer plastic jar of 0.86 mm thickness, 680 ml capacity, 7.59 cm mouth diameter and 11.7 cm deep was first placed in the ground. This outer jar which had a hole for draining flood water from the inner cup was installed once and remained in the ground for the two-year sampling period.

The inner cup was removed once monthly and a clean cup with collecting fluid placed in the outer jar again. The cup and its contents were put in another 550 ml plastic container with a 10.0 cm diameter, 8.0 cm deep and 0.27 mm thick making them very light to carry. The container was then closed tightly with a lid to facilitate transportation of samples to the laboratory without spilling. The lids had been permanently marked with trap numbers.

In the laboratory, the contents of the trap were then emptied into a white plastic tray with a 30 cm diameter. A 60 watt bulb was shone through the tray. With the aid of forceps and water sprayed through a laboratory water bottle the leaves and debris and soil were sorted out carefully to ensure that specimens were not missed.

3.2.3 Pitfall trap installation

A hole in the ground for the outer jar was created using a small strong rock pry easy to carry around with a long pointed stiff blade to cut through small roots and pry rocks without bending and was very efficient in hard difficult soils. Secateurs (pruning clippers) were used to cut away any roots sticking out in the hole before the outer jar was placed inside. Heavy duty leather gloves were worn to protect the hands from being hurt by digging and handling sharp roots, stones and thorns. Knee-length rubber boots protected the legs from any other dangers like snake bites and sharp objects on the ground. A metal slasher was used to gain initial access into very thick overgrown bush-forest and very tall grassland

habitats. Once the outer jar was placed into the hole, a garden trowel was used to push the soil firmly around it. The inner cup was then placed firmly inside the outer cup and it was then made sure that this inner cup was flush with the ground using soil to fill space around it, otherwise the animals are partially deterred (Gist and Crossley 1973; Luff, 1975, 1996; Halsall and Wratten, 1988)

It was also found that to ensure maximum trap efficiency, areas prone to flooding during heavy rains were either avoided or traps were placed at positions that were not directly in line with the path of flood water flow.

The problem of relocating traps after initial placement was overcome using trap markers made of red bricks. The soil was dug up and the brick placed permanently into the ground surface along a path to indicate that the trap was somewhere in that vicinity. Very conspicuous markers were avoided as they tended to attract curious vertebrates such as humans and monkeys who then destroyed or disturbed the traps.

3.2.4 Pitfall trap roofing

To keep out debris and water during heavy rains, a roof constructed from deep PVC guttering found in hardware stores was used. It was cut into a table-like shape of 15 cm by 11 cm by 7 cm creating openings into the trap from four sides Fig. 3.1 (b). Because of heavy wind, the roof was weighted down with a stone.

3.2.5 Collecting fluid

Ethylene glycol (ethanediol) also known as antifreeze has been reported to be the best collecting fluid for long intervals and is currently the collecting fluid of choice especially in the northern hemisphere (Morill, 1975; Van den Berghe, 1992; Bedford and Usher, 1994; Kajak and Lukasiewicz, 1994; Niemela *et al.*, 1993; Eversham and Telfer, 1994). It is a viscous liquid which does not evaporate easily due to its high boiling point (194°C-199°C) and is therefore suitable for long interval use in the hot Savanna areas. It has properties which lower the freezing point of water (Packer and Vaughan, 1958) and therefore finds use as an anti-freeze agent which enables its use during winter. Traps were filled with 100 ml of one part ethylene glycol and one part water.

It is also used as an antifreeze coolant for motor-vehicle engines and is therefore easily available in

petrol service stations even in the developing world. Its alcohol properties make it a good preservative for specimens as it keeps specimens caught at monthly intervals fresh.

The use of formalin was abandoned because it is highly toxic and requires extra caution when transporting and handling in the field. Although the use of a saturated salt solution was tried as salt is very cheap and easily available, it was not suitable in the hot Savanna areas as it dried out completely during hot days.

3.2.6 Collecting the trap catch

Traps were serviced every two weeks and the trap catch collected after 4 weeks. It was found that the highest beetle activity coincided with the rainy summer months. After heavy rains some traps tended to fill up with soil, debris and water there was a high risk of losing specimens caught in the traps as it was not possible to see them through muddy flood waters in the traps. In addition the rain water diluted the collecting fluid and reduced its preservation ability which resulted in the decomposition of the specimens in traps. To avoid losing specimens this way, traps were routinely visited every two weeks and serviced by replacing with a new cup and collecting fluid and taken to the lab to be sorted before they started to rot. After a particularly heavy downpour, traps would be serviced the following day.

Servicing also involved the fixing of other forms of disturbance to the traps caused by monkeys that would pull the trap cups out, traps that were placed in the path of a mole would be dug out and therefore another site would have to be found. Large animals like giraffe and zebra would crash the traps with their feet and small animals like moles and rabbits would dig around the trap and disturb the flushness of the trap mouth with the ground making the trap to be very inefficient. The unevenness of the trap mouth with the ground was also caused by certain soil types which when dry would form cracks and collapse around the trap mouth and this were repaired by patching up this cracks with soil from the surrounding and bringing the trap mouth level with the ground.

Trap catches were collected and sorted after four weeks because it was found that in all sites except the macadamia plantation, where carabid abundance was very high, there was hardly any carabids trapped after two weeks and that waiting for an additional two weeks increased the number of catches, saved on the frequent replacement of the collecting fluid and saved on transport cost of visiting the sites when operating on a tight budget.

The total catch of 4197 individuals of carabids and cicindelids over the whole study period of two years from June 1994 to May 1996 would not have been achieved had it not been for a thorough dedication to trap servicing to ensure maximum trapping efficiency, as pointed out by Luff (1996).

3.3 METHODS

To determine the carabid and cicindelid point distributions, four forest and four grassland habitats along an altitude-gradient transect across two geographical zones in the study area were sampled. See Chapter 2 for a full description of the sites. Carabids and cicindelids were recorded over the eight sites by pitfall trapping and visual searching. This was done over a period of two years from June 1994 to May 1996 covering two seasons.

3.3.1 Pitfall trap sampling

Sampling was at points which were chosen using the stratified random sampling method (Samways, 1983, 1990; Williams, 1987). Each point was a particular habitat within the site and was selected taking into account parameters such as vegetation type, nearness to river or swamp, middle or bottom of hill.

Each of the 32 point habitats was sampled using a set of four pitfall traps representing the corners of a 1.5 metre square, Fig.3.2. The set of four traps represents a point sample of carabids replicated four times. These sets were placed 10 metres to about 500 metres apart within sites, and from about 0.1 km to 20 km among sites. This was done to determine the heterogeneity within and across sites in the study area. Each of the eight sites had four point habitats, giving the total 32 point habitats or sampling units, with 128 pitfall traps in the whole study area.

The traps were installed at the beginning of the month of June 1994 and were serviced every two weeks by removing any litter, debris and any other form of obstruction. Trap contents were collected at the end of every month by removing the inner trap and taking it to the laboratory where they were sorted and counted. Monthly counts took place until May 1996, giving a total of 24 monthly replicates.

3.3.2 Window trap sampling

3.3.2.1 Glass window traps

Window traps described by Southwood (1978) were used to maximise catches of ground beetles that

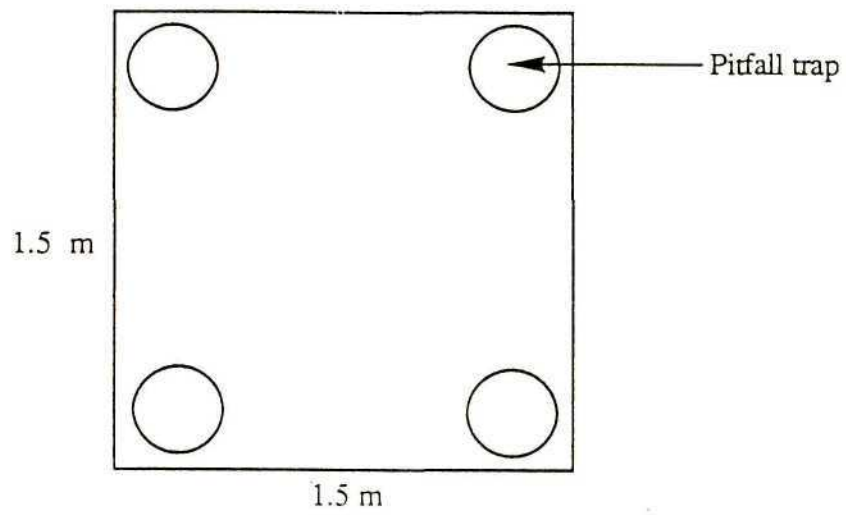


Figure 3.2: A point habitat comprising a set of four pitfall traps at the corners.

fly. The traps were installed over September to March (1994/1995) during summer. Four square glass window traps (30 cm by 30 cm) placed one metre above the ground were installed at various point habitats within each site. After a period of six months, there were no carabids and cicindelids trapped in the forest habitats. Only cicindelids were trapped in the grassland habitat at Site 4 (which is subjected to frequent burning). A total of four individuals belonging to two species as *Dromica gilvipes* and *Cicindela marginella inanis* were trapped (Table 4.1). The pitfall method caught more individuals and species of carabids and cicindelids than this window trap method. Therefore this method was abandoned after six months.

3.3.2.2 PVC-netting material window trap

Another window trap made of PVC-netting material two metres long was employed during the same period. Four traps were placed within each site. They were installed in the natural forests at S1 and S5 with great difficulty owing to the nature of thick bush within these forests. After seven months this technique caught no carabids nor cicindelids in any of the forest and grassland habitats. This type of window trap was very conspicuous and was very frequently disturbed. In addition, it required more volume of collecting fluid than pitfall traps. Therefore, this window trap method was abandoned after six months.

3.3.3 Visual sampling

Visual sampling was carried out during the summer months of October, November, December, January and February 1994/1995 when beetle activity was at peak level. This involved searching randomly under decaying plant material such as logs and leaf-litter in the forest habitats and through open patches and tufts of grass in grassland habitats. Stones turned over were replaced after searching to minimize disturbance of the environment. Each site had two hours of searching in a day from 10.00 am to 12.00 pm and was done two times in a month for five months in a year thus giving a total of forty hours of searching over the two years sampling period. Total number of individuals per species counted was recorded.

3.3.4 Environmental variables

The great majority of carabid and cicindelid species are terrestrial, and in South Africa, relatively few species are arboreal hunters (Scholtz and Holm, 1986). The ground-inhabiting species are often encountered in moist places and others live under decaying plant material such as logs or leaf-litter, and some prefer open sandy patches among tufts of grass or stones. The eggs are laid in the soil. The larvae are active free living predators with well developed legs for running or burrowing. Pupation takes place in the ground or in a sheltered spot under cover of stones or logs. Considering adult and larval requirements, ten major environmental variables were recorded (Table 3.1) but only eight of them were employed in the multivariate analysis (Table 3.2) in Chapter 4. This was because the other two variables not used in the analysis namely, soil texture and sand grade were found to be highly correlated with the quantity of sand in the A1 horizon.

The environmental variables were grouped into quantitative variables and nominal variables. The nominal variables specify a classification of samples and the values are thus classes (Ter Braak, 1988). The five quantitative variables were: (1) sand in the A1 horizon (%), (2) pH of soil, (3) soil moisture (%), (4) twigs and/or leaf litter cover (%) and (5) shade cover (%). The three major nominal variables and their classes were: geographical location based on altitude as (6) Escarpment-E and (7) Savanna-S; habitat type based on level of community succession as (8) primary forest-PF, (9) secondary forest-SF, (10) secondary grassland-SG, (11) primary grassland; management regime based on type of land-use as (12) nature management-NM, (13) pine plantation-PP, (14) recreational park-(PA), (15) grassland road verges-RV, (16) macadamia plantation (orchard)-MP, (17) grassland field-FD.

3.3.4.1 Soil texture analysis

Soil texture and sand grade was measured by determining the amount of sand, silt and clay present in the soil. This was done using the Hydrometer Method (Martin, 1993). The separated soil components were then classified in accordance with the UK classification 1976 system (William, 1987).

Percentage sand in the A1 horizon was the value that was eventually used in the ordination analysis because it was viewed as an index defining a moisture-nutrient regime (Peet and Loucks, 1977). The final value shown in Table 3.1 and Table 3.2 is the average of seven by two replicates taken over 1994 (December), 1995 (June, August, November, December); 1996 (February, March).

	S1				S2				S3				S4			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Sand in Al horizon (%)	35.56	35.56	59.31	59.31	44.73	44.72	44.74	44.73	61.00	61.72	61.72	61.73	66.10	66.12	66.11	66.10
pH of soil	3.77	3.76	4.73	4.74	3.66	3.65	3.65	3.66	4.26	3.97	3.97	3.97	3.99	4.00	3.99	3.99
Soil moisture (%)	4.63	4.63	2.50	2.50	3.73	3.73	3.73	3.73	2.73	2.72	2.72	2.72	2.10	2.10	2.11	2.11
Litter cover	3	3	3	3	3	3	3	3	1	1	2	2	1	1	1	1
Shade	9	9	9	9	8	8	8	8	0	0	5	5	0	0	0	0
Geographical region	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E
Habitat type	PF	PF	PF	PF	SF	SF	SF	SF	SG	SG	SG	SG	PG	PG	PG	PG
Management regime	NM	NM	NM	NM	PP	PP	PP	PP	PA	PA	PA	PA	RV	RV	RV	RV
Soil texture	CL	CL	SL	SL	CL	CL	CL	CL	SL	SL	SL	SL	SL	SL	SL	SL
Sand grade	FS	FS	CS	CS	CS	CS	CS	CS	CS	MS	MS	MS	CS	CS	CS	C

	S5				S6				S7				S8			
	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Sand in Al horizon (%)	25.64	25.64	17.64	10.96	23.15	23.10	23.15	23.15	31.78	38.43	38.43	31.78	21.00	21.01	21.11	21.00
pH of soil	5.71	5.71	6.15	5.58	5.32	5.31	5.32	5.32	6.40	6.45	6.45	6.40	5.06	5.06	5.00	5.06
Soil moisture (%)	7.62	7.62	8.33	6.55	4.31	4.31	4.31	4.32	3.55	5.26	3.26	3.55	5.07	5.06	5.08	5.07
Litter cover	3	3	3	3	1	1	1	1	2	2	2	2	1	1	1	1
Shade	9	9	9	9	0	0	0	0	9	0	0	9	0	0	0	0
Geographical region	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
Habitat type	PF	PF	PF	PF	PG	PG	PG	PG	SF	SF	SF	SF	SG	SG	SG	SG
Management regime	NM	NM	NM	NM	RV	RV	RV	RV	MP	MP	MP	MP	FD	FD	FD	FD
Soil texture	L	L	CL	SIC	SCL	SCL	SCL	SCL	SL	CL	CL	SL	C	C	C	C
Sand grade	CS	CS	FS	FS	FS	FS	FS	FS	CS	CS	CS	CS	CS	CS	CS	CS

Table 3.1: Environmental data arranged for the 32 point habitats in the whole study area. Each of the eight sites (S1 to S8) has four point habitats, e.g. S1 (1, 2, 3, 4). The scores of the environmental variables in column one, are explained in the text, Section 3.3.4. Escarpment (E); Savannah (S); Primary Forest (PF); Secondary Forest (SF); Secondary Grassland (SG); Primary Grassland (PG); Nature Management (NM); Pine Plantation (PP); Park (PA); Road Verge (RV); Macadamia Plantation (MP); Grassland Field (FD); Clay Loam (CL); Sandy Loam (SL); Loam (L); Silty Clay (SIC); Silty Clay Loam (SCL); Clay (C); Fine Sand (FS); Medium Sand (MS); Coarse Sand (CS).

Site	Sand in A1 horizon (%)	pH of soil	Soil moisture (%)	Litter cover	Shade	Geographical region	Habitat type	Management regime
1	47.44	4.25	3.57	3.0	9.0	E	PF	NM
2	44.73	3.66	3.73	3.0	8.0	E	SF	PP
3	61.54	4.04	2.72	1.5	2.5	E	SG	PA
4	66.10	3.99	2.10	1.0	0.0	E	PG	RV
5	19.97	5.79	7.53	3.0	9.0	S	PF	NM
6	23.15	5.32	4.31	1.0	0.0	S	PG	RV
7	35.11	6.43	3.41	2.0	4.5	S	SF	MP
8	21.00	5.06	5.07	1.0	0.0	S	SG	FD

Table 3.2: Environmental data as mean values of the four point habitats per site (Table 3.1) arranged for each of the eight sites (1 - 8). The scores are explained in the text (Section 3.3.4).

3.3.4.2 Soil water analysis

A soil sample was first air dried at room temperature until completely dry. It was then broken up in a pestle and mortar to disperse the soil particles. It was then sieved through a 2000 µm sieve. Two replicates of 10 grams of the air dried sample was then put in an oven at 105°C overnight to drive off the water. It was then placed in a desiccator and allowed to cool before weighing. The weight loss on drying was then expressed as a percentage water content of the total soil weight.

The final value shown in Table 3.1 and Table 3.2 is the average of seven by two replicates taken over 1994 (December), 1995 (June, August, November, December); 1996 (February, March).

3.3.4.3 Soil pH analysis

Two replicates of 10 grams of a ground sieved and air dried soil sample was used. 25 ml of distilled water was added. It was allowed to stand for 30 minutes with occasional stirring and then the pH value of the supernatant liquid was measured using a glass Electrode pH metre. The final value shown in Table 3.1 and Table 3.2 is the average of seven by two replicates taken over 1994 (December), 1995 (June, August, November, December); 1996 (February, March).

3.3.4.4 Leaf and/or twig litter cover

Total area of ground covered by litter for each point habitat was determined and scored on a three-point scale. The measurement scale used was an ordinal scale described by (Van der Maarel, 1979; Jongman *et al.*, 1987). Point habitats covered with twigs and leaf litter all year round were given a score of 3, e.g. S1, S2 and S5. Point habitats covered with leaf litter for at least three months in a year (before being cleaned away) were given a score of 2, e.g. S7. Point habitats covered with leaf litter for less than a month to two months before being cleaned away were given a score of 1.5, e.g. S3. Those point habitats with no leaf litter e.g. grasslands at S4, S6 and S8 were given a score of one.

3.3.4.5 Shade determination

Shade was based on estimates of the mean percentage shade cover at midday over summer and winter, for each point habitat. The proportion of soil shaded from sunlight by vegetation present was estimated. The Braun-Blanquet transformation (Jongman *et al.*, 1987) was carried out on the mean percentage data

and scored on a 10 point scale. For example, 0 to 5 % cover was given a score of zero and 96 to 100% cover was given a score of 10.

3.3.4.6 Geographical location

Two elements were studied and classified as nominal variables of Escarpment at high altitude of 900 metres above sea level and Savanna at lower altitude of 700 metres above sea level. Climate data covering monthly averages of maximum temperature, rainfall and maximum relative humidity were recorded from the following weather stations situated within the study area; (i) Ukulinga Agricultural Research Station situated at 29° 40'S 30° 24'E having an altitude of 775 metres with a Savanna climate, Appendix 1 Table 3.3. (ii) Cedara Agricultural Research Station situated at 29° 32'S 30° 17'E having an altitude of 1067 metres with an Escarpment climate, Appendix 1 Table 3.4.

3.3.4.7 Habitat type

There were four 'habitat types' which correspond with pairs of the eight sites described in detail in Chapter 2.

Primary forest (PF) was a climax forest comprising primary or plagioclimax species which has not been severely disturbed is corresponding with S1, a natural indigenous forest at high elevation and S5, an *Acacia*-dominated woodland at low elevation.

Secondary forest (SF) was a planted woodland occupying a site that was formerly unwooded land. This corresponds with a pine plantation S2, at high elevation and a macadamia plantation (orchard) S7, at low elevation.

Primary grassland (PG) was a term used here to describe the two roadside verge sites at high elevation S4 and low elevation S6 which were composed of mostly native grasses and burnt each autumn in a way that mimics natural events.

Secondary grassland (SG) was a term used here to describe the two grasslands which were regularly mown. These correspond to the recreational grassland park (S3), at high elevation and the field grassland (S8) that was harvested for hay once every year at lower elevation.

3.3.4.8 Management regime

This was a classification of sites as a nominal variable (Jongman *et al.*, 1987; Ter Braak, 1988) based on type of land use as; (12) nature management-NM, (13) pine plantation-PP, (14) recreational park-(PA), (15) grassland road verges-RV, (16) macadamia plantation (orchard)-MP, (17) grassland field-FD.

3.3.5 Mean body sizes

A stereoscopic microscope with micrometer eyepiece for measuring was used. The body length from the front of the head to end of elytra was measured, (Forsythe, 1987). Twenty individuals were measured for the most abundant species. Ten individuals of a species were selected randomly from the total catch of each year for the two years. For the rare species, all individuals collected were measured.

Geometric mean was used in the determination of mean body size and not arithmetic mean because geometric means take into consideration random variation or stochastic effects (Blake *et al.*, 1994; Krebs 1994; Primack, 1998).

3.4 DATA ANALYSIS

3.4.1 Introduction

Data were analysed in two steps. Firstly, univariate methods for species abundance relationships covering diversity indices and distribution models. Secondly, multivariate techniques of classification and ordination. More than one technique was carried out in each step which provided a learning experience in various methods of community data analysis in addition to providing an opportunity to compare various methods for confirming the results obtained. Ludwig and Reynolds (1988) and Jongman *et al.*, (1987) have recommended the use of more than one method in ecological community data analysis.

In the analysis of this results, patterns across the first sampling season (June 1994-May 1995), second sampling season (June 1995-May 1996), and as a sum of the two seasons (June 1994-May 1996) are reported.

3.4.2 Univariate methods

3.4.2.1 Diversity indices

The full set of species counts per site was reduced into single coefficients to enable comparisons. The Rarefaction model for species richness (Ludwig and Reynolds, 1988), which measures the number of different species for a fixed number of individuals was used to compare sites. Margalef's (R1) index was also used. Diversity numbers presented by (Hill, 1973) were used. They are in units of number of species and measure what Hill calls the effective number of species present in a sample as a degree to which proportional abundances are distributed among the species. $N0=S$, where S is the total number of species in a sample; $N1=e^{H'}$, where H' is Shannon's index and N1 is a measure of abundant species. $N2=1/\lambda$, where λ is Simpson's index and N2 is a measure of very abundant species. Simpson's index λ has values ranging from 0 indicating high diversity to 1 indicating low diversity. It is a measure of the probability that two individuals drawn at random from a population belong to the same species. Shannon's index H' is a measure of the average degree of uncertainty in predicting to what species an individual chosen at random from a collection of S species and N individuals will belong. When $H'=0$ it means there is one species in the sample indicating low diversity. H' is maximum indicating high diversity when all S species are represented by the same number of individuals, i.e a perfectly even distribution of abundances. Pielou's Evenness Index J' was used. Although calculations of diversity indices may not be valid when based on pitfall data rather than actual population densities, it has been shown that multivariate analysis of data from sampling programmes that have been conducted under standardized conditions can lead to meaningful results (Luff *et al.*, 1992; Dufrene and Legendre, 1997).

3.4.2.2 Representing communities by graphical methods

Temporal changes in species abundance across monthly replicates and for each site was represented graphically. The indices of species richness, diversity (H'); and evenness (J') were also presented graphically.

3.4.2.3 Determining stress levels using Caswell's neutral model

The evenness component of diversity can however, be compared with some theoretical expectation of diversity, given the number of individuals and species present. Observed diversity has been compared

with predictions from Caswell's neutral model (Caswell, 1976). This model constructs an ecologically 'neutral' community with the same number of species and individuals as the observed community, assuming certain community assembly rules (random births/deaths and random immigration/emigrations) and no interactions between species. The deviation statistic V is then determined which compares the observed diversity (H') with that predicted from the neutral model ($E(H')$). A value of zero for the V statistic indicates neutrality, positive values indicate greater diversity than predicted and negative values lower diversity. Values greater than +2 or less than -2 indicate significant departures from neutrality (Caswell, 1976). The computer program Caswell in PRIMER (Clarke and Warwick, 1994) was used to compute the V statistic for the eight sites using carabid and cicindelid species data.

3.4.2.4 Distribution models: lognormal, rank abundance and x2 geometric plots

Relationships between abundance and the number of species having that abundance was shown graphically using plots of abundance of each species in the community in order of its rank from the most to the least abundant for each of the eight sites. The lognormal model, x2 geometric plots and rank abundance curves were used to obtain various information from the distribution patterns for each site.

The lognormal distribution model was carried out as described in Ludwig and Reynolds (1988) so as to estimate (i) S^* which is the theoretical number of species available for observation per site and therefore the species unobserved in the community, and (ii) determine the nature of communities at each site. Other distributional models, namely x2 geometric species abundance plots, and ranked species abundance or dominance curves, were used to detect the effects of disturbance or stress at each site. Gray and Pearson (1982) have reported that, in undisturbed situations, there are many rare species giving smooth curves with the mode well to the left. In disturbed situations there are fewer rare species and more abundant species, so that the higher geometric abundance classes are more strongly represented, giving more irregular curves. They have also suggested that it is the species in the intermediate abundance classes 3 to 5 that are the most sensitive to pollution induced changes and might best illustrate the differences between polluted and unpolluted sites and therefore a way of selecting 'indicator species' objectively.

3.4.2.5 Correlation

Spearman correlation coefficients were used to measure the association between climate variables and species abundance and richness. These correlations were calculated with SPSS 6.1.

3.4.3 Multivariate methods

Although the sampling design would allow for analysis of variance-type approaches, the presence of many zeros in the data especially at the plot level made this approach not suitable. This problem was solved by the use of ordination techniques in multivariate analysis. Classification and ordination methods were used to analyse patterns within the communities in the whole study area. These methods are characterised by the fact that they base their comparisons of samples on the extent to which these samples share particular species, at comparable levels of abundance. Similarity coefficients calculated between every pair of samples help facilitate a classification or clustering of samples into groups which are mutually similar or an ordination plot in which the samples are 'mapped' into multidimensional space in such a way that the distances between pairs of samples reflect their relative dissimilarity of species composition.

3.4.3.1 Classification

Divisive classification method or fuzzy clustering of sites is the exact opposite of hierarchical agglomerative clustering used here. All methods had been tried giving similar results. In addition results of clustering have to be confirmed further by ordination methods (Ludwig and Reynolds, 1988, Clarke and Warwick, 1994). I decided to report results of hierarchical agglomerative clustering only and carry out two ordination methods (NMDS and CA/CCA) instead. A method of hierarchical agglomerative clustering using the computer programme "Cluster" which is in the computer software PRIMER an acronym of **P**lymouth **R**outines **I**n **M**ultivariate **E**cological **R**esearch (Clarke and Warwick, 1994) was used.

The species by sample unit (SU) data matrix was transformed using 4th root transformation to balance rarer and common species. The Bray-Curtis similarity coefficient co-variance based was then used on these data to produce a similarity matrix and then fused successively through hierarchical clustering using group average linking . The results of this clustering were represented by a dendrogram with the

x axis representing the full set of samples and the y axis defining a similarity level at which two samples or groups are considered to have fused.

Because clustering can be misleading, especially where there is a steady gradation in community structure across sites, perhaps in response to strong environmental gradient, ordination method was therefore carried out so as to confirm and describe the community patterns in the study area.

3.4.3.2 Ordination

Ordination is a term used to describe a set of techniques in which SUs are arranged in relation to one or more coordinate axes such that their relative positions to the axes and to each other provide maximum information about their ecological similarities. When SUs that are most similar or dissimilar are identified based on coordinate positions, underlying biotic and abiotic factors that might be responsible for the observed patterns are determined.

Two ordination techniques were employed for carabid and cicindelid species data, namely Non Metric Multidimensional Scaling (MDS) using the computer software PRIMER (Clarke & Warwick, 1994), and Correspondence Analysis (CA) and Canonical Correspondence Analysis (CCA) using the computer software CANOCO, an acronym of **CAN**onical **C**ommunity **O**rdination (Ter Braak, 1988)

3.4.3.2.1 Ordination of samples by MDS using PRIMER

Although CANOCO and PRIMER tackle similar ecological problems, they use different techniques. For comparison purposes, the following ordination methods in PRIMER were used to link environmental variables to species data.

i) Analysis of environmental data by PCA using PRIMER

PCA (Principal Components Analysis) was used in the multivariate analysis of SUs by environmental data matrix. PCA is more appropriate to environmental variables because the data have no large blocks of zero counts needing to be treated in a special way. It is no longer necessary to select a dissimilarity coefficient that ignores 'joint absences', and therefore Euclidean distance measure is used. In addition, environmental data have a complex mix of measurement scales or units, and to solve this problem a correlation-based PCA was carried out to normalise all axes so that they have comparable dimensionless

scales.

A 2-dimensional (2-D) PCA plot of the environmental variables, transformed and normalised, for the eight SUs was carried out. The total percentage variance explained by the first two components was then determined in order to ascertain whether the 2-D picture provides an accurate summary of the sample relationships.

ii) Linking biota patterns produced by MDS to univariate community measures using PRIMER

Because biotic data are best described by a multivariate summary ordination such as Non-metric Multi-dimensional Scaling (MDS), its relation to a univariate environmental measure can then be visualised by representing the values of this variable as symbols of differing size and superimposing these symbols on the biotic ordination of the corresponding samples. This is a very effective means of noting any consistent differences in the environmental variable between biotic clusters or observing a smooth relationship with ordination gradients (Field *et al.*, 1982).

Superimposing each environmental variable onto ordination was carried out for carabids and cicindelids together to determine the role of individual taxa in shaping the biotic picture (Warwick and Clarke, 1993).

These plots, however, make clear the limitations in relating the community structure to a single environmental variable at a time. Questions like "How well does the full set of abiotic data jointly explain the observed biotic pattern?" and "Is there a subset of the environmental variables that explains the pattern equally well or better?" are limited. These questions can be answered in classical multivariate techniques such as Canonical Correlation, but Clarke and Warwick, (1994) point out that this requires assumptions which are unrealistic for species abundance data (Correlation and Euclidean distance as measures of similarity for biota, linear relationships between abundance and environmental gradients etc.). Instead, the need is to relate community structure to multivariate descriptions of the abiotic variables using the type of non-parametric, similarity-based methods.

iii) Linking biotic patterns produced by MDS to multivariate environmental patterns using PRIMER

The intuitive premise adopted here is that if the suite of environmental variables responsible for structuring the community were known, then samples having rather similar values for these variables

would be expected to have rather similar species composition, and an ordination would group sites in the same way as for the biotic plot. If key environmental variables are omitted, the match between the two plots will deteriorate. By the same token, the match will also worsen if abiotic data which are irrelevant to the community structure are included.

An MDS ordination plot of the eight sites based on species abundance data, was compared with MDS plots of all the environmental variables together and specific combinations in order to determine the 'best fitting' environmental combination to the biota plot i.e the combination that best explains the community pattern.

For consistency of presentation the environmental variable plots are also MDS ordinations but based on an appropriate dissimilarity matrix (Euclidean distance on the normalised abiotic variables).

iv) Comparison of biotic and abiotic variables using the Bio-env program of PRIMER

Quantifying the match between any two plots was done using Procrustes analysis (Gower, 1971) in which one plot is rotated, scaled or reflected to fit the other, in such away as to minimise a sum of squared distances between the superimposed configurations.

The ranks for the Bray-Curtis similarity matrix for biota and the Euclidean distance matrix for environmental variables are compared through a weighted Spearman rank correlation coefficient ρ_w (Kendall, 1970). ρ_w lies in the range -1 to 1 where the two sets of ranks are in complete opposition or complete agreement values of ρ_w around zero correspond to the absence of any match between the two patterns. The computer program Bio-env in PRIMER was used to carry out this test.

3.4.3.2.2 Ordination of samples by CA/CCA using CANOCO

The computer software CANOCO (Ter Braak, 1988), which combines into one algorithm detrended correspondence analysis(DCA) on species data with weighted multiple regression on environmental data, was used. CANOCO and MDS (described in section 3.4.3.2.1 above) tackle essentially similar problems, though using different techniques.

This multivariate analysis technique (CANOCO) relates community composition to known variation in the environment. The technique is an extension of correspondence analysis (reciprocal averaging),

a popular ordination technique that extracts continuous axes of variation from species occurrence or abundance data (Ter Braak, 1986). Such ordination axes are typically interpreted with the help of external knowledge and data on environmental variables: this two-step approach (ordination followed by environmental gradient identification) is termed indirect gradient analysis. In canonical correspondence analysis, ordination axes are chosen in the light of known environmental variables by imposing the extra restriction that the axes be linear combinations of environmental variables. In this way community variation can be directly related to environmental variation. The environmental variables may be quantitative or nominal. As many axes can be extracted as there are environmental variables. The method of detrending can be incorporated in the technique to remove arch effects, however this was found not to be applicable to the data here.

CANOCO leads to an ordination diagram in which points represent species and sites and vectors represent environmental variables (Gabriel, 1971, 1981, Hill, 1979, Gauch, 1982ab, Ter Braak, 1983). Such a diagram shows the patterns of variation in community composition that can be explained best by the environmental variables and also visualizes approximately the “centers” of the species distributions along each of the environmental variables (Ter Braak and Looman, 1986). Such diagrams effectively summarized relationships between community and environment for datasets on hunting spiders (Smeenk-Enserink, 1975, Ter Braak, 1986), dyke vegetation (De lange, 1972, Ter Braak, 1986), algae along a pollution gradient (Fricke and Steubing, 1984, Ter Braak, 1986), dragonflies (Steytler and Samways, 1995).

Monte Carlo Permutation tests to determine the degree of significance of the effect of particular environmental variables on community composition taking into account the effect of other variables were also carried out.

3.5 Beetle identification

The expertise of Dr. Endrödy Younga at the Transvaal Museum, Pretoria, South Africa and keys to tribe, genera and species (Ball, 1971; Arnett, 1971; Freude *et al.*, 1976; Endrödy, 1978; Scholtz and Holm, 1986), were used in the identification of the beetles. The resulting reference or voucher specimens are deposited at the Transvaal Museum, Durban Museum and at the Invertebrate Conservation Research Centre, University of Natal Pietermaritzburg.

CHAPTER 4

RESULTS

4.1 SAMPLING METHODS

4.1.1 Numbers of species and individuals caught

Each species was assigned a code number in the order in which a new beetle was found during sampling (Table 4.1). Throughout the text, these code numbers have been used in brackets after a species is mentioned, e.g. *Metagonum gilvipes* (115a). This has been employed as a quick reference to the actual species name in Table 4.1.

Table 4.1 contains a list of 37 species from nine tribes and nine subfamilies which were collected over the whole sampling period. A total of 4197 individuals in 35 species were collected by pitfall traps and only an additional two individuals of two further species, namely *C. impictus* (157) and *C. fasciger* (45b), were collected by visual searching. Glass window traps caught four individuals of two species that had been collected by pitfall trapping. PVC-netting window traps caught nothing.

Out of 37 species collected, four were cicindelids. One out of the four cicindelid species was undescribed, and six out of 33 carabid species were undescribed.

During the first sampling season (June 1994 to May 1995), a total of 2312 individuals in 29 species of carabids and cicindelids were collected, and 1885 individuals in 26 species were collected over the second sampling season (June 1995 to May 1996).

4.1.2 Window trapping

4.1.2.1 Glass window traps

Window traps (Southwood, 1978) were used in an attempt to maximise catches of ground beetles

FAMILY	TRIBE	GENUS	SPECIES	CODE NUMBERS	
CICINDELIDAE	Cicindelini	<i>Cicindela</i>	<i>marginella</i> Dej. (spp) <i>inanis</i> (Wallengr.)	7	
		<i>Dromica</i>	<i>tuberculata</i> Dej. (spp) <i>carinulata</i> (Chaud.)	14	
		<i>Dromica</i>	<i>gilvipes</i> Boh.	250a	
	*	*	*	250b	
CARABIDAE	Graphipterini	<i>Graphipterus</i>	<i>cordiger</i> Dej. (spp) <i>subhamatus</i> (Basil.)	240a	
	Panagaeini	<i>Craspidophorus</i>	<i>impictus</i> Boh.	157	
			<i>bonvouloiri</i> Chaud.	252	
	Pterostichini	<i>Cophosomorpha</i>	<i>pseudocastellani</i> Str.	38	
		<i>Metagonum</i>	<i>gilvipes</i> Boh.	115a	
		<i>Euleptus</i>	<i>caffer</i> Boh.	115a-w	
		<i>Abacetus</i>	*	213	
	Oodini	<i>Systolocranius</i>	<i>alternaris</i> Chaud.	254	
	Axinidiini	<i>Metaxinidium</i>	<i>nanum</i> Basil.	140	
	Lebiini	*	*	*	32
		<i>Lebia</i>	<i>nematopeza insidiosa</i> (Pering.)	130a	
			<i>immaculata</i> Chaud.	240b	
			*	155	
		<i>Pentagonica</i>	<i>gracilis</i> Pering.	130b	
		<i>Hystrihopus</i>	<i>atratus</i> Chaud.	147	
			<i>mniszewski</i> Pering.	105	
		<i>Metaxymorphus</i>	<i>atriceps</i> Pering.	181	
		<i>Poecilothais</i>	<i>tetragramma</i> Chaud.	257	
	Chlaenini	<i>Chlaeniostenus</i>	<i>cylindricus</i> Dej.	40a	
		<i>Pachydinodes</i>	<i>simplex</i> Wied.	40b	
			<i>bipustulatus</i> Boh.	256	
		<i>Stenodinodes</i>	<i>fenestratus</i> Chaud.	45a	
		<i>Chlaenius</i>	<i>fasciger</i> Chaud.	45b	
			<i>vitticollis</i> Boh.	154	
		<i>Callistomimus</i>	<i>caffer</i> Boh.	178	
	Harpallini	*	*	35a	
		*	*	35b	
		*	*	115b	
		*	*	122	
		<i>Hyparpalus</i>	<i>tomentosus</i> Dej.	133	
		*	*	126	
		*	*	150	
*	*	243			
*	*	*	276		

Table 4.1: Species list of Carabidae and Cicindelidae collected over the whole study period. Undescribed species (*). Illustrations of some of these species can be seen in Appendix 3.

that fly. But after a period of six months, no carabids or cicindelids were trapped in any of the forest habitats. Only cicindelids were trapped in the grassland habitat at Site 4, which was subjected to frequent autumn burning. A total of four individuals belonging to two species, *Dromica gilvipes* (250a) and *Cicindela marginella inanis* (7), were trapped. Indeed, these two species were observed to have short bursts of flight when disturbed. The pitfall method caught more individuals and species of carabids and cicindelids than this window trap method. Therefore, this method was abandoned after six months.

4.1.2.2 PVC-netting material window trap

This traps were installed in the natural forests at S1 and S5 with great difficulty due to the nature of thick bush within these forests. After six months, this technique caught no carabids nor cicindelids in any of the forest and grassland habitats. This type of window trap was very conspicuous and were frequently disturbed by humans. In addition, they required more volume of collecting fluid than pitfall traps. Therefore, this window trap method was abandoned after six months.

4.1.3 Visual searching

This involved searching randomly under decaying plant material such as logs and leaf-litter in the forest habitats and through open patches and tufts of grass in grassland habitats. Stones turned over were replaced after searching to minimize disturbance of the environment. It was generally observed that individuals were easily seen over the morning hours than the afternoon hours. Even the most abundant species among the leaf litter in macadamia plantation were absent among the litter in the afternoons but were abundant among the litter in the morning hours before noon.

4.1.3.1 Visual searching in the natural indigenous mistbelt forest (S1)

A total of 21 individuals of two species were observed. The most common species *M. gilvipes* (115a) was observed under logs than among the leaf litter. A total of three individuals of *Systolocranius alternaris* (254) were also observed among the leaf litter.

4.1.3.2 Visual searching in the pine plantation (S2)

A total of 32 individuals of five species were observed. Fourteen individuals of the most common *Abacetus* sp. (213) was observed in leaf litter. Other species observed were *Hystrichopus mniszewski* (105), *M. gilvipes* (115a), *Pachydinodes simplex* (40b) and Harpalini sp. (115b). They were mostly present among heaps of pruned decomposing branches (Fig. 2.3).

4.1.3.3 Visual searching in the recreation park (S3)

A total of ten individuals of two species were observed. The two most common species, *M. gilvipes* (115a) and *Stenodinodes fenestratus* (45a), were observed in the leaf litter and under stones used for landscaping.

4.1.3.4 Visual searching in the road verge grassland (S4)

A total of 35 individuals of four cicindelids species (Table 4.1) and 11 individuals of one carabid species, *Graphipterus subhamatus* (240a), were observed. These species were all observed within the first 30 minutes of searching among the open grass patches induced by fire burning and by grass cutting along electricity posts. All the four cicindelid species were observed to have short bursts of flight when disturbed. Mating was observed in *Cicindela inanis* (7) and in *Dromica carinulata* (14). Following is a description of a behaviour observed in *C. inanis* (7). This species, was seen flying about in the grass and tended to rest on the warm concrete slabs in the road verge from time to time. On one of these concrete slabs, two of these beetles were seen walking on either side of the concrete slab and stopping at intervals to forage. When these two beetles reached a few centimetres from each other, they suddenly pounced at each other and started to fight. But flew away when they were disturbed. Another pair of this species were also seen mating on the concrete slab.

4.1.3.5 Visual searching in the Acacia-dominated woodland (S5)

A total of three species were observed. *Pachydinodes bipustulatus* (256) was observed under decaying logs, while *M. gilvipes* (115a) was found under stones near the river. Many individuals of Harpalini sp. (35b) aggregated among the wet sand in the river bed. The most dominant Carabidae sp. (243) caught by pitfall trapping was not seen in visual searches.

4.1.3.6 Visual searching of the road verge grassland (S6)

Although no beetles were observed during visual searching in the grasslands at this site, they were however caught in the pitfall traps.

4.1.3.7 Visual searching in the macadamia plantation (S7)

The undescribed species from the Harpalini tribe with code numbers (126, 115b, 150) were common and aggregated in huge numbers among the leaf litter at this site. Other species observed were *M. gilvipes* (115a) and *Hyparpalus tomentosus* (133).

4.1.3.8 Visual searching in the grassland field (S8)

Species not recorded by pitfall traps but found at this site by visual searching were *C. impictus* (157) and *C. fasciger* (45b). These species were on stalks of grass rather than on the ground surface. Otherwise, other species caught in this site by pitfall trapping were not seen while carrying out a visual search.

4.1.4 Pitfall trapping

All the analyses in this study have been carried out using pitfall trapping species data. Table 4.1 illustrate a list of species collected over the whole study period. Tables 4.2 - 4.26 Appendix 2, contains species data. Specifically, Tables 4.2 - 4.9 and Tables 4.11- 4.18 list the species and their abundances at monthly intervals, arranged for each point habitat across the eight sites. Tables 4.10, 4.19 and 4.20 illustrate numbers of species at monthly intervals arranged for the first, second and both of the two sampling seasons respectively. Table 4.21 illustrate numbers of individuals and species, in each of the eight sites as a sum of two seasons. Tables 4.22 and 4.23 lists numbers of individuals and species, in each of the eight sites arranged for the first and second sampling seasons respectively. Tables 4.24, 4.25 and 4.26 illustrate species and individuals arranged for each point habitat in each of the eight sites.

4.2 SPECIES CUMULATIVE CURVES

4.2.1 Species cumulative curve over two annual sampling seasons

Table 4.20 Appendix 2, shows the cumulative number of species recorded over two seasons and arranged for each of the 12 monthly samples for the whole sampling area. Fig. 4.1 (a) is a graphical presentation of this information. Thirty five species were recorded, and the curve reached its asymptote on the 11th sampling replicate (i.e. April) using sum of data from two annual sampling seasons (June 1994- May 1995 and June 1995 - May 1996). There was a high increase of species recorded over the spring and summer months of September through to March (19 to 34) and an additional increase of one species over winter.

4.2.2 Species cumulative curves for each annual sampling season

Tables 4.10 and 4.19 Appendix 2, show the cumulative number of species recorded over the first sampling season (June 1994 to May 1995) and second sampling season (June 1995 to May 1996) for the whole sampling area. Fig. 4.1 (b) compares the two seasons. During the first season 1994/1995, 29 species were recorded, and the curve reached its asymptote by the 10th sampling replicate in March. In the second sampling season, 26 species were recorded and the curve reached its asymptote by the 11th sampling replicate in April. There was a high increase of species collected over the spring and summer months of September to March. Four additional species were collected over the winter of the second season and none over the first season's winter.

4.2.3 Species cumulative curves at each of the eight sites

Table 4.29 is a summary of data on cumulative number of species obtained from Tables 4.2 to 4.20 Appendix 2 and Fig. 4.1 (c). From this table, it can be seen that most species were collected over the summer months of September to March at each of the eight sites. Except for Site 4 and Site 8, very few (1, 2 or 3) additional new species were caught over winter at each site. Comparisons in the rate of numbers caught at each site varied across sampling seasons.

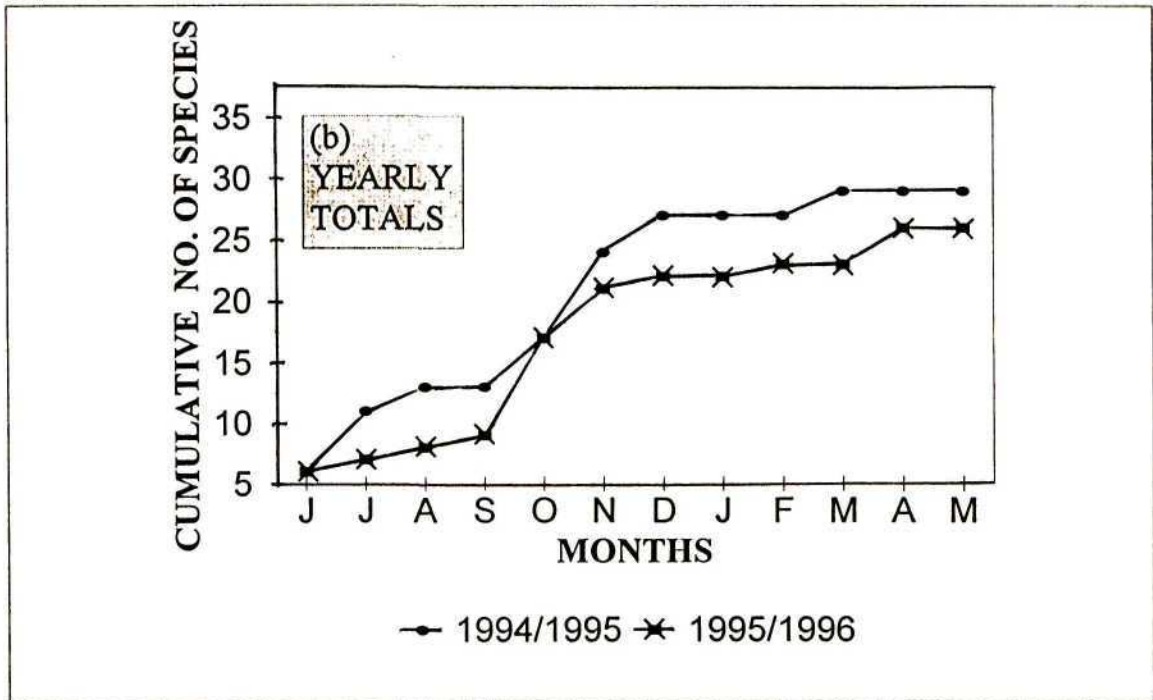
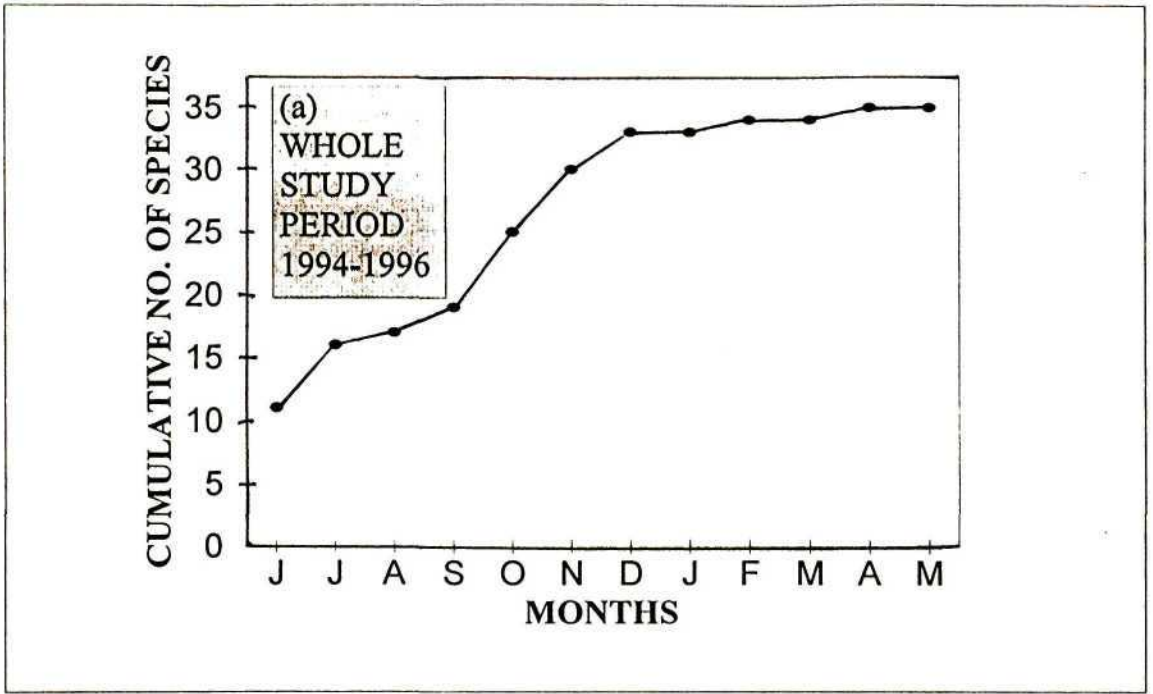


Figure 4.1: (a) Cumulative number of species recorded over two sampling seasons (June 1994 - May 1995) and (June 1995 - May 1996), for the whole sampling area. (b) Cumulative number of species recorded over the first sampling season (June 1994 - May 1995) and the second sampling season (June 1995 - May 1996) for the whole sampling area.

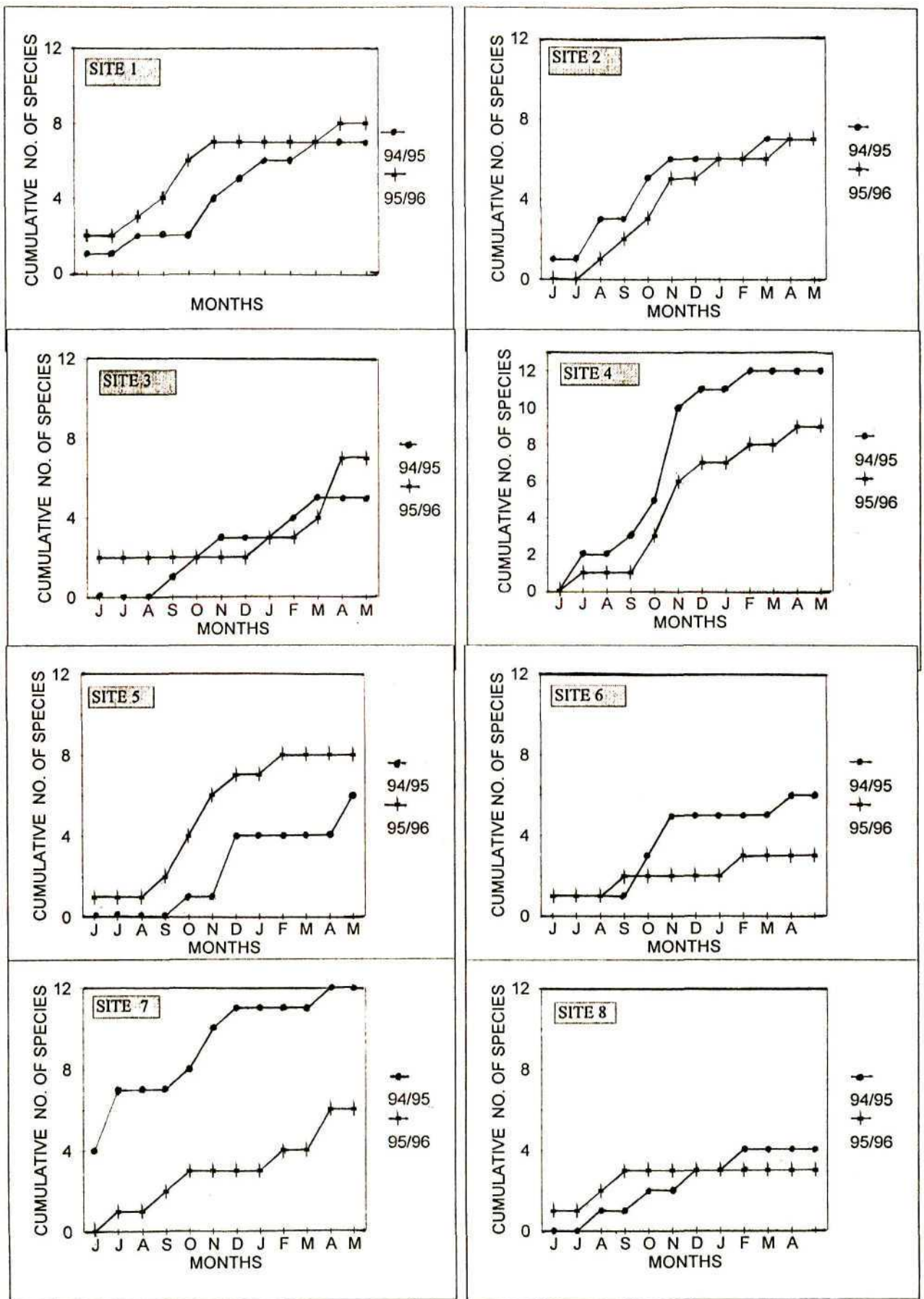


Figure 4.1(c): Cumulative number of species recorded over the first sampling season (June 1994-May 1995) and the second sampling season (June 1995-May 1996), shown for each of the eight sites (1-8).

4.3 SEASONAL POPULATION VARIATION

4.3.1 Seasonal population variation at all sites

The general climate pattern per year or per season in the whole study area is as follows; June/July (winter); August/September (spring); October, November, December, January, February, March (summer); April/May (autumn).

Table 4.20 Appendix 2 shows the sum of the number of individuals recorded over two seasons and arranged for each of the 12 monthly samples, for the whole sampling area. Tables 4.10 and 4.19 Appendix 2 show the number of individuals recorded over the first sampling season (June 1994 to May 1995) and second sampling season (June 1995 to May 1996) respectively.

Fig. 4.2 (a, d) gives the rainfall patterns across the 24 monthly samples for Escarpment and Savanna climates. The Escarpment Zone received more average annual rainfall (860 mm), than the Savanna Zone (688 mm) and both Zones had higher rainfall in the second season than in the first season. Data on humidity and temperature (Tables 3.3 and 3.4) showed an increase in values from winter to summer and then remaining almost constant over summer, when beetle activity was also high. Spearman correlation coefficients used to measure the association between climate variables and species abundance and richness were all positive (Tables 4.1.1 and 4.1.2), but not all statistically significant.

The Escarpment during the first sampling season (1994/1995) received 584.5 mm of rain, and 439 individuals of 20 species were recorded. The second season received 1134.7 mm of rain and a total 561 individuals of 18 species were recorded. The Savanna during the first sampling season (1994/1995) received 633.5 mm of rain, and 1873 individuals of 16 species were recorded. The second season received 780 mm of rain, and a total 1324 individuals of 13 species were recorded. Therefore, it appears that, in the Escarpment Zone high rainfall over the second season caused an overall increase in abundance but a drop in number of species. In the Savanna Zone, an increase

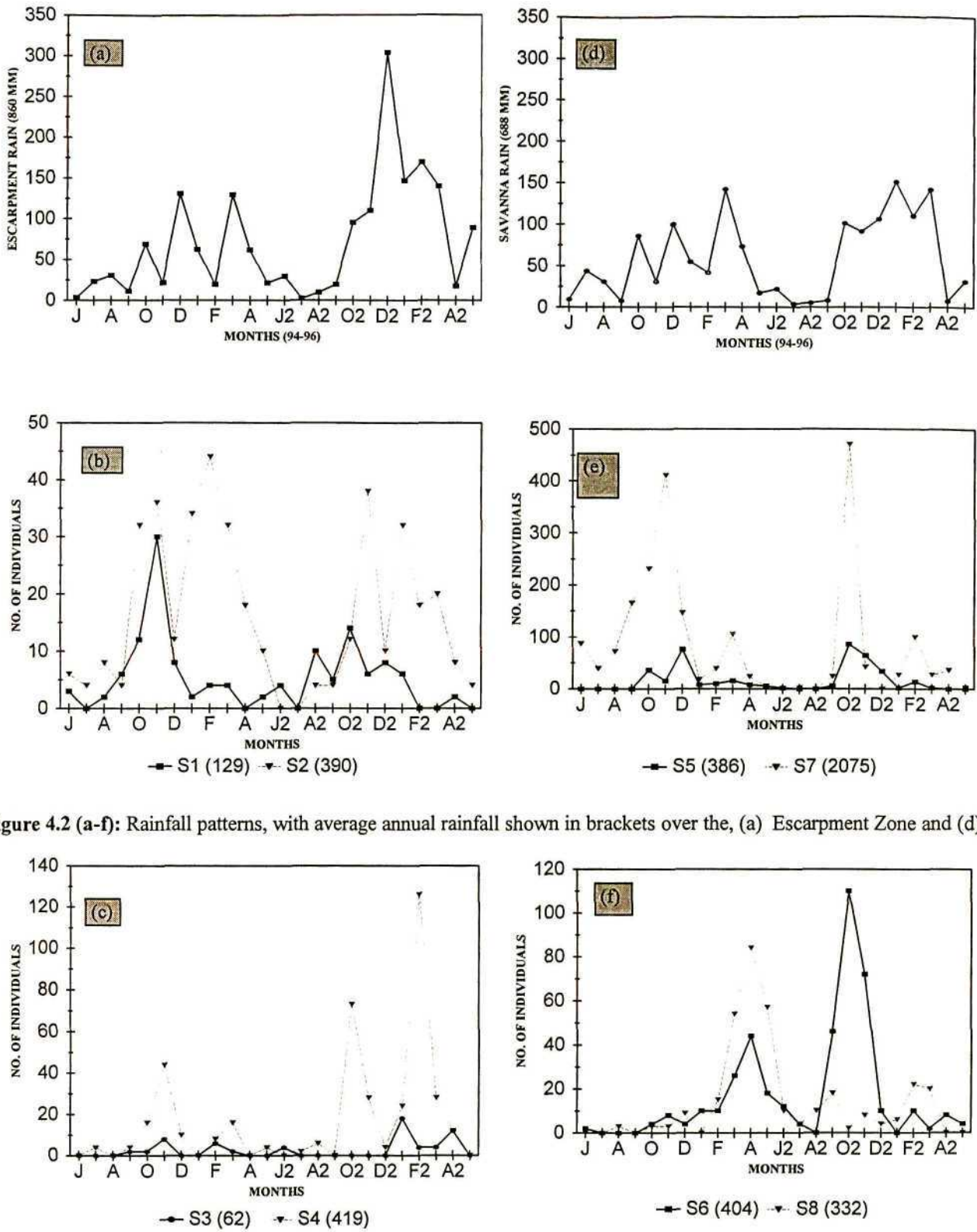


Figure 4.2 (a-f): Rainfall patterns, with average annual rainfall shown in brackets over the, (a) Escarpment Zone and (d)

Savanna Zone. Number of individuals of carabids and cicindelids across twenty four monthly sampling replicates from June 1994-May 1996, is shown for sites within the Escarpment Zone as S1, S2, S3, S4 (b, c) and within the Savanna Zone as S5, S6, S7, S8 (e, f). Total number of individuals collected per site over the whole sampling period is shown in brackets, e.g. S1(129). Months over the second sampling season are shown with the number 2, e.g. J2.

	First season (June 1994-May 1995)				Second season (June 1995-May 1996)				Sum of two seasons (June 1994-May 1996)			
	Rain (mm)	Temp. (°C)	Humidity (%)	Abundance (n)	Rain (mm)	Temp. (°C)	Humidity (%)	Abundance (n)	Rain (mm)	Temp. (°C)	Humidity (%)	Abundance (n)
Temp. (°C)	0.24				0.57				0.51			
Humidity (%)	0.66*	0.36			0.55	0.49			0.57	0.28		
Abundance (n)	0.24	0.14	0.19		0.45	0.53	0.31		0.34	0.32	0.18	
Species (n)	0.56	0.48	0.28	0.49	0.36	0.23	0.49	0.82**	0.64*	0.32	0.30	0.69*

Table 4.1.1: Spearman correlation coefficients (calculated with SPSS 6.1) between climate and species in change in species abundance and richness over monthly samples ($n=12$), for two annual sampling seasons and as a sum of both seasons, in forest and grassland sites within the Savanna Zone. Significance at the $P=0.05$ level is shown by (*) and Significance at the $P=0.01$ level is shown by (**).

	First season (June 1994-May 1995)				Second season (June 1995-May 1996)				Sum of two seasons (June 1994-May 1996)			
	Rain (mm)	Temp. (°C)	Humidity (%)	Abundance (n)	Rain (mm)	Temp. (°C)	Humidity (%)	Abundance (n)	Rain (mm)	Temp. (°C)	Humidity (%)	Abundance (n)
Temp. (°C)	0.25				0.62*				0.69*			
Humidity (%)	0.68*	0.26			0.59*	0.36			0.66*	0.25		
Abundance (n)	0.29	0.74**	0.56		0.65*	0.70*	0.62*		0.70*	0.78**	0.51	
Species (n)	0.38	0.61*	0.47	0.84**	0.48	0.45	0.65*	0.84**	0.72**	0.54	0.61*	0.87**

Table 4.1.2: Spearman correlation coefficients (calculated with SPSS 6.1) between climate and species in change in species abundance and richness over monthly samples ($n=12$), for two annual sampling seasons and as a sum of both seasons, in forest and grassland sites within the Escarpment Zone. Significance at the $P=0.05$ level is shown by (*) and Significance at the $P=0.01$ level is shown by (**).

in rainfall in the second season appeared to cause a drop in beetle abundance as well as a drop in the number of species recorded.

Fig. 4.2 (b c e f) shows beetle abundance in the Savanna and Escarpment Zones across the two seasons. Fig.4.2 (a to f) shows that beetle abundance was positively correlated with rainfall patterns, and increases with rainfall to a certain point and then drops when rainfall becomes high e.g. December 1995 (D2) when there was high rainfall causing flooding and resulting in a big drop in beetle activity and/or a drop in trap efficiency.

The rainfall pattern had two peak periods per annual season, both in the Escarpment and Savanna Zones. In the Escarpment Zone, the first peak was from September to January, with maximum rainfall in December, (i.e. 130 mm in December of the first season and 304 mm in December of the second season). In the Savanna Zone, the first peak was from September to January with maximum rainfall in January, (i.e. 99 mm in January of the first season and 151 mm in January of the second season). The second annual rainfall peak was from February to May. This second rainfall peak in the Escarpment Zone, had maximum rainfall in March, (i.e. 130 mm in the first season and 169 mm in February in the second season). In the Savanna Zone, the second annual rainfall peak had maximum rainfall in March (i.e. 141 mm in the first season and 141 mm in March of the second season).

There are also two beetle activity peaks in the Escarpment Zone. The first peak in the Escarpment Zone was from September to December, with maximum numbers recorded in November ($n=118$) over the first sampling season and in October ($n=99$) in the second season. The second peak in the Escarpment Zone was from January to May with maximum numbers recorded in February ($n=62$) over the first sampling season and in February ($n=158$) in the second season.

There are also two beetle activity peaks in the Savanna Zone. The first was from July to January, with maximum numbers recorded in November ($n=438$) over the first sampling season, and in October ($n=669$) in the second season. The second peak in the Savanna Zone was from January to

May, with maximum numbers recorded in March ($n=201$) over the first sampling season, and in February ($n=145$) over the second season.

The troughs indicating very low beetle activity occurred in June-July (winter) and about December-January (mid-summer) for both the Escarpment and Savanna Zones. This suggests that there is a period in mid summer when beetle activity is reduced either because species become dormant or heavy rains that fall during this period reduce beetle activity or traps become less efficient. This can only be explained if the life cycles of individual species are known.

There was variation in the number of individuals collected over each sampling season per month. Therefore, the altitudinal difference of about 200 metres between the Escarpment and Savanna Zones does not have an effect on peak beetle activity periods and rainfall peak periods across the two Zones. But the 200 metres difference between Escarpment and Savanna Zones does influence total climate in terms of total rainfall, temperature and humidity and vegetation type which, in turn, appear to determine species assemblages.

4.3.2 Comparison of seasonal population variation between forests and grasslands at the same altitude

Tables 4.2 - 4.20 Appendix 2 give the numbers of individuals recorded over the first and second sampling seasons for all the eight sites. Fig. 4.2 (b, c, e, f) is a graphical presentation of this information.

4.3.2.1 Seasonal population variation in natural indigenous forest (S1) and pine plantation forest (S2) at high altitude

The natural forest (S1) and pine plantation (S2) had similar beetle activity patterns (Fig. 4.2), but S2 had higher overall abundance than S1.

At S1, three species out of ten made up 75% of the total catch over the two sampling seasons. The order of decreasing dominance was *M. gilvipes* (115a) 38%, *Lebiini* sp. (32) 34% and *Cophosomorpha pseudocastellani* (38) 11%. At S2, four species out of eight recorded made up 93% of the total catch. The order of decreasing dominance was *Abacetus* sp. (213), *Lebiini* sp. (32) 32%, *C. pseudocastellani* (38) 32%, *Lebiini* sp. (32) 15%, *Harpalini* sp. (35a) 14%. Site 1 therefore had fewer dominant species and many rare ones, whereas S2 had many dominant species and relatively fewer rare ones.

A Mann-Whitney U-test carried out to test the abundances of similar species across S1 and S2 namely, *M. gilvipes* (115a), *Lebiini* sp. (32), *C. pseudocastellani* (38) and *Abacetus* sp. (213) showed a significant difference ($P < 0.05$) in the distribution of these species at these two sites. For example, *M. gilvipes* (115a) was more abundant at S1 than S2 and *Abacetus* sp. (213) and *C. pseudocastellani* (38) was more abundant at S2 than S1. *Harpalini* sp. (35a) was only recorded at S2.

The number of individuals varied from one season to the next. Three new species were recorded at S1, and one new species at S2 in the second season (Tables 4.2-4.3 and Tables 4.11-4.12 Appendix 2).

4.3.2.2 Seasonal population variation in a recreational park grassland (S3) and a road verge grassland (S4) at high altitude

The two grassland habitats show similar beetle activity patterns but S4 had higher overall abundance than S3. The park site (S3) with management of lawn kept mown throughout the year had lower beetle activity compared to the road verge (S4) with autumn burning management.

At S3, one species, *M. gilvipes* (115a) out of the eight species recorded, made up 42% of the total. The rest of the species were in very low abundance with a high turnover, i.e. they were present in the first season but absent in the following season or they were absent in the first season and present in the following season. For instance, five new species were recorded at S3 in the second season.

Site 3 shared more species with S1 and S2 than it did with S4, maybe due to it being adjacent to S1 and S2 (see Fig. 2.2) and may have had vagrant species from S1 and S2. Also the nature of disturbances at S3 and S4 were different. However, it appears that the intensively managed park is an unstable habitat for carabids.

At S4, four out of 14 species made up 78% of the total. These species were *Euleptus caffer* (115a-w) 40%, *M. gilvipes* (115a) 13%, *Graphipterus subhamatus* (240a) 13% and *Cicindela inanis* (7) 12%. Site 4 received autumn burning at the beginning of the first season and no burning in the second season. As a result, the overall abundance over the first season was much lower ($n=106$) than over the second season ($n=313$). There were five species recorded in the first season with burning but were absent in the second season without burning, likewise two new species were only recorded in the second season. For example, *E. caffer* (115a-w) was present only in the tall grasses that had grown after burning. All the cicindelid species were recorded at this site and they were abundant in summer, in all the four point habitats over the first sampling season after autumn burning (Table 4.5 Appendix 2). During the second sampling season, without burning, all the cicindelids recorded were only present in the point habitat number 13, which had received cutting of grass, and were absent in the rest of the point habitats that had tall grasses (Table 4.14 Appendix 2). Therefore it appears that burning and or cutting disturbance in autumn initiates successional stages in grasslands that are suitable for different species.

Overall order of decreasing beetle abundance of forest and grassland sites within the Escarpment Zone was: road verge grassland (S4), pine plantation (S2), primary indigenous forest (S1), park (S3). Therefore the intensity and type of disturbance, in addition to the type of habitat and seasonal climatic changes seem to influence the number of individuals at a given site over time.

4.3.2.3 Seasonal population variation in Acacia-dominated woodland (S5) and macadamia plantation (S7) at low altitude

The natural *Acacia*-dominated forest (S5) and the macadamia plantation (S7) have different species

assemblages but similar beetle activity patterns (Fig. 4.2), with S7 having a higher overall abundance than S5.

At S5, two species, Carabidae sp. (243), with 77% dominance and *Hystrichopus mnischechi*, with 11% dominance), out of a total number of 11 species, made up 88% of the catch over the two sampling seasons. The rest of the species were in low abundance, with high species turnover across the two seasons (Tables 4.6 and 4.15 Appendix 2). There were three species recorded in the first season that were absent from the second season, e.g. two individuals of the cicindelid species *D. gilvipes* which was more abundant in the adjacent grassland of S6 in the first season after autumn burning was recorded at point habitat number 18 at S5 which was situated nearer to the border with S6. In addition some parts of S5 situated on the edge with S6 had burnt, as a result this cicindelid species found preferred habitats on the edge of landscape S5. Likewise five new species were recorded in the second season that were absent from the first.

At S5, during the first season, the Carabidae sp. (243) comprised 76% of the total of six species and was recorded from October to March with a high peak activity in December followed by reduced activity over January and February then by a small activity peak over March, (Table 4.6 Appendix 2). In the second season, the Carabidae sp. (243) comprised 79% of the total of eight species and was recorded from September to December with a peak activity in October, (Table 4.15 Appendix 2). Heavy rain over December to March in this period may be the reason for the absence of activity of this Carabidae sp. (243). This species was bigger in size relative to the rest of the species caught at S5. In the second season, the overall number of species ($n=8$) and abundance ($n=210$) and rainfall (780 mm) was higher than in the first season, with number of species ($n=6$), abundance ($n=176$) and rainfall (634 mm). This observation shows that rainfall increases species abundance and the presence of shelter sites provided by trees, herbs and thick layer of leaf and twig litter on the ground in this landscape, protects the beetles from the adverse effects of heavy rainfall. Therefore factors that might be influencing species abundance at S5 are spill over burning from the border grasslands at S6 and seasonal variations in rainfall.

Site 7 is a monoculture of macadamia plantation under agricultural management dominated by species from the Harpalini tribe. Four species out of 13 recorded made up 94% of the total. The order of decreasing dominance at S7 was Harpalini sp. (126) 45%, Harpalini sp. (115b) 33%, Harpalini sp. (150) 16%. S5 and S7 had different carabid species assemblages. There was little variation in the dominant species across the two sampling seasons at S7. In the first season the overall species ($n=12$) and abundance ($n=1343$) was higher than in the second season with species ($n=6$), abundance ($n=732$). On the other hand rainfall was lower (634 mm) in the first season and higher (780 mm) in the second season, especially over the months of December to March with no beetles recorded in December although there was a mid-summer trough of reduced activity around January in both seasons for the most abundant species (Tables 4.8 and 4.17 Appendix 2). One of the reasons for this was the absence of deep shelter to the ground from tree canopy which was more open and therefore exposed more to weather effects like rain. In addition, leaf litter was from time to time removed from the ground during the year leaving the ground bare. Another reason for this low activity over mid-summer could be a dormant period of the adults.

In addition, over the winter months of June and July, ($n=126$) individuals of beetles were recorded at S7 over the first sampling season when the ground leaf litter was very high, (Table 4.8 Appendix 2) but nothing was recorded at S5 (Table 4.6 Appendix 2).

4.3.2.4 Seasonal population variation in a road verge grassland (S6) and a field grassland (S8) at low altitude

The two grassland habitats comprising a managed road verge that had been subjected to autumn burning (S6) and (S8) being a mediumly managed field of hay mown once a year that borders macadamia plantation (S7) showed the following patterns. Similar peak beetle activity periods but different abundance patterns (Fig. 4.2), with S6 having a higher overall abundance than S8.

Both S6 and S8 had a higher abundance over late summer during the first season (Fig. 4.2), except this pattern changed at S6 during the second season because of the increased dominance of a single

Carabidae sp. (243) that was not dominant in the first season. At S6 the intensity of autumn burning over the first season was higher thus resulting in a different species assemblage e.g. presence of *D. gilvipes* and low numbers of Carabidae sp. (243) comprising 25% of the total catch over the first season as opposed to an increase in abundance over the second season comprising 86% of the total catch.

The carabid assemblage at S8 was more similar to that of the adjacent S7, than to the one at S6. For example, the two most dominant species at S7 were Harpalini sp. (126) 45%, Harpalini sp. (115b) 33%. At S8, it was Harpalini sp. (115b) 72%, Harpalini sp. (126) 14%. At S6, it was Carabidae sp. (243) 66%, Harpalini sp. (115b) 21%. The nature of disturbance being autumn burning at S6 and cutting once a year at S8 influenced the pattern at each site.

Overall order of decreasing beetle abundance in forest and grassland sites within the Savanna Zone was: macadamia forest (S7), road verge grassland (S6), *Acacia* woodland (S5), field of hay (S8). Therefore the nature and intensity of disturbance, type of vegetation and seasonal variations influenced species assemblages at a given site.

4.3.3 Comparison of seasonal population variation between primary and secondary forests and grasslands

4.3.3.1 Seasonal population variation in primary forests: natural indigenous forest (S1) and Acacia-dominated woodland (S5)

The natural indigenous tree dominated forest (S1) at high altitude and S5 an *Acacia*-dominated forest at low altitude have similar peak activity periods across the two sampling seasons but different species assemblages. *M. gilvipes* (115a) was common to both forests but reached maximum abundance in S1. The species *Lebia insidiosa* (130a) was exclusively recorded at S5 and S1 in very low abundance.

There were a few beetles collected over winter (June /July) in both sites. During winter, in S1, a total of seven individuals of three species were recorded, namely *M. gilvipes* (115a), *M. nanum* (140) and *H. atratus* (147), (Tables 4.2 and 4.11 Appendix 2). At S5, two individuals of one species *L. immaculata* (240b) was recorded (Tables 4.6 and 4.15 Appendix 2).

Overall the primary *Acacia*-dominated landscape S5 at low altitude had a higher beetle abundance ($n=386$) than the primary indigenous forest S1 ($n=129$) at high altitude. The species assemblages in the two sites were different. There was little variation in the assemblage composition within each landscape across seasons. Therefore vegetation type, altitude, seasonal variations and nature of management at each site appear to determine species assemblages more than habitat type as primary forest.

4.3.3.2 Seasonal population variation in secondary forests: pine plantation (S2) and macadamia plantation (S7)

Pine plantation (S2), situated at high altitude and macadamia plantation (S7) situated at low altitude had different species assemblages, but both sites had two peak beetle activity periods per season. At S7 the first peak over September to December was relatively higher than the second peak over January to May. At S2 the two peaks are relatively equal (Fig. 4.2). This may be due to the fact that troughs in these sites appeared in December when rainfall was heavy at both sites across the two seasons, but the effect of rainfall was more severe to the fauna at S7, which had a more open tree cover and no herb cover than at S2 which had a more closed tree cover and some herb cover that provided shelter to the ground fauna during heavy rains.

Macadamia plantation (S7) had the highest recorded beetle abundance ($n=471$) in October of the second season and S2 had only ($n=44$) as highest recorded in February of the first season. At both sites beetles were recorded throughout the year.

Overall the secondary macadamia plantation forest landscape at low altitude, had a high beetle

abundance ($n=2075$) than the secondary pine plantation ($n=390$) at high altitude. The species assemblages in the two sites are different. There was little variation in the assemblage composition within each landscape across seasons. Therefore vegetation type, altitude, seasonal variations and nature of management at each site appear to determine species assemblages more than habitat type as secondary forest.

4.3.3.3 Seasonal population variation in primary grasslands: a road verge (S4) and a road verge (S6)

Site 4 situated at high altitude with autumn burning over the first season and S6 with autumn burning situated at low altitude have beetle activity periods with similar peaks. Species assemblages between the two sites became more similar in the first season when both sites received autumn burning, even though they were at different altitudes. Species common to these sites were, *D. gilvipes* (250a), Harpalini sp. (115b), *C. caffer* (178), Harpalini sp. (126).

The total abundance over the first season was S4 ($n=106$) and S6 ($n=126$) and the abundance over the second season was S4 ($n=313$) and S6 ($n=278$). Highest beetle abundance was ($n=126$) in February at S4 in the second season and S6 had ($n=110$) individuals in October of the second sampling season. At both sites the second season had received less disturbance than the first season. Overall the road verge primary grassland (S4) at high altitude had a high beetle abundance ($n=419$) than the road verge grassland S6 ($n=404$) at low altitude.

Therefore, since the type of disturbance and vegetation types at these two grasslands were similar it can be said that, the factors influencing the species assemblages at these sites are the intensity of disturbance, seasonal variations and climate.

4.3.3.4 Seasonal population variation in secondary grassland: recreational park (S3) and a field of hay (S8)

Site 3, a park at high altitude and S8, a field of hay mown once a year at low altitude, have almost similar activity patterns of low abundance from June to December and high abundance from January through to April at S3 and to May at S8. The reason for this observation may be that, S8 received mowing in autumn which provided less shelter for species. Towards the end of the season, over late summer, the grass had grown again returning the shelter. Site 8 had a higher beetle abundance ($n=84$) in April of the first sampling season and S3 had only $n=18$ as highest recorded in January of the second sampling season. Overall the moderately managed grassland field (S8) at low altitude had a high beetle abundance than the intensively managed park grassland (S3) at high altitude.

The species assemblages at these two sites were very different. The only two species shared between the two sites was the Harpalini sp. (115b) and Harpalini sp.(35a). Otherwise, these grasslands shared more species with the forest sites which were adjacent to them, i.e. S3 was more similar to S1 and S2 than it was to S8. Likewise S8 was more similar to S7 than it was to S3.

4.3.4 Seasonal population variation as number of species

Table 4.20 Appendix 2 shows the sum of the number of species recorded over two seasons and arranged for each of the 12 monthly samples for the whole sampling area. Tables 4.2-4.19 Appendix 2 shows the number of species recorded over the first sampling season (June 1994 - May 1995) and second sampling season (June 1995 - May 1996) respectively. Fig. 4.3 (a) compares the two seasons for each of the eight sites.

The graphs (Fig. 4.3a) show similar patterns observed in Fig. 4.2 (b, c) and (e, f) as number of individuals over monthly replicates. It is clear from the graphs that number of species recorded over months increases with increasing abundance. This is further supported by highly significant ($P=0.05$ and $P=0.01$ in the Savanna and Escarpment Zones respectively) Spearman correlation values

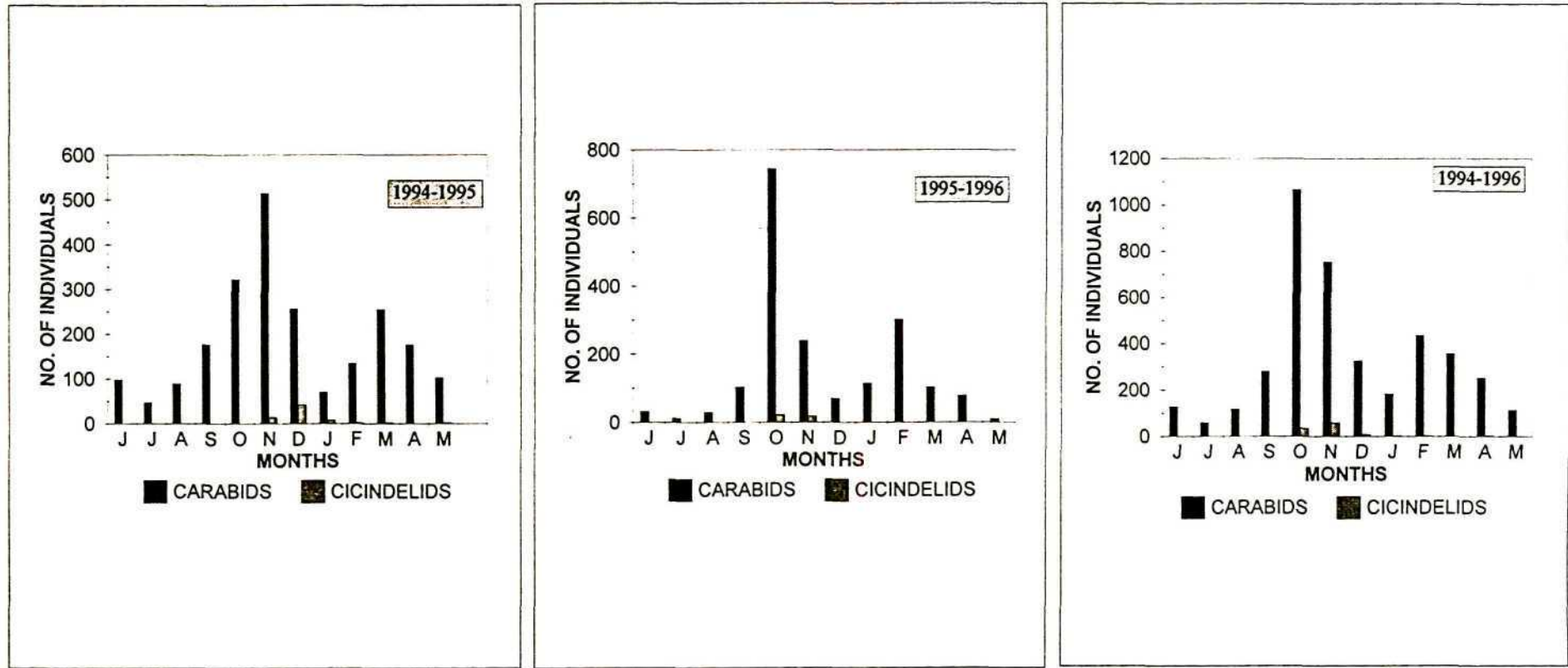


Figure 4.2(g): Proportional abundance of carabids and cicindelids recorded over the first sampling season (June 1994-May 1995), the second sampling season (June 1995-May 1996) and as the sum of the two seasons (June 1994-May 1996), arranged for each of the 12 monthly replicates, for the whole sampling area.

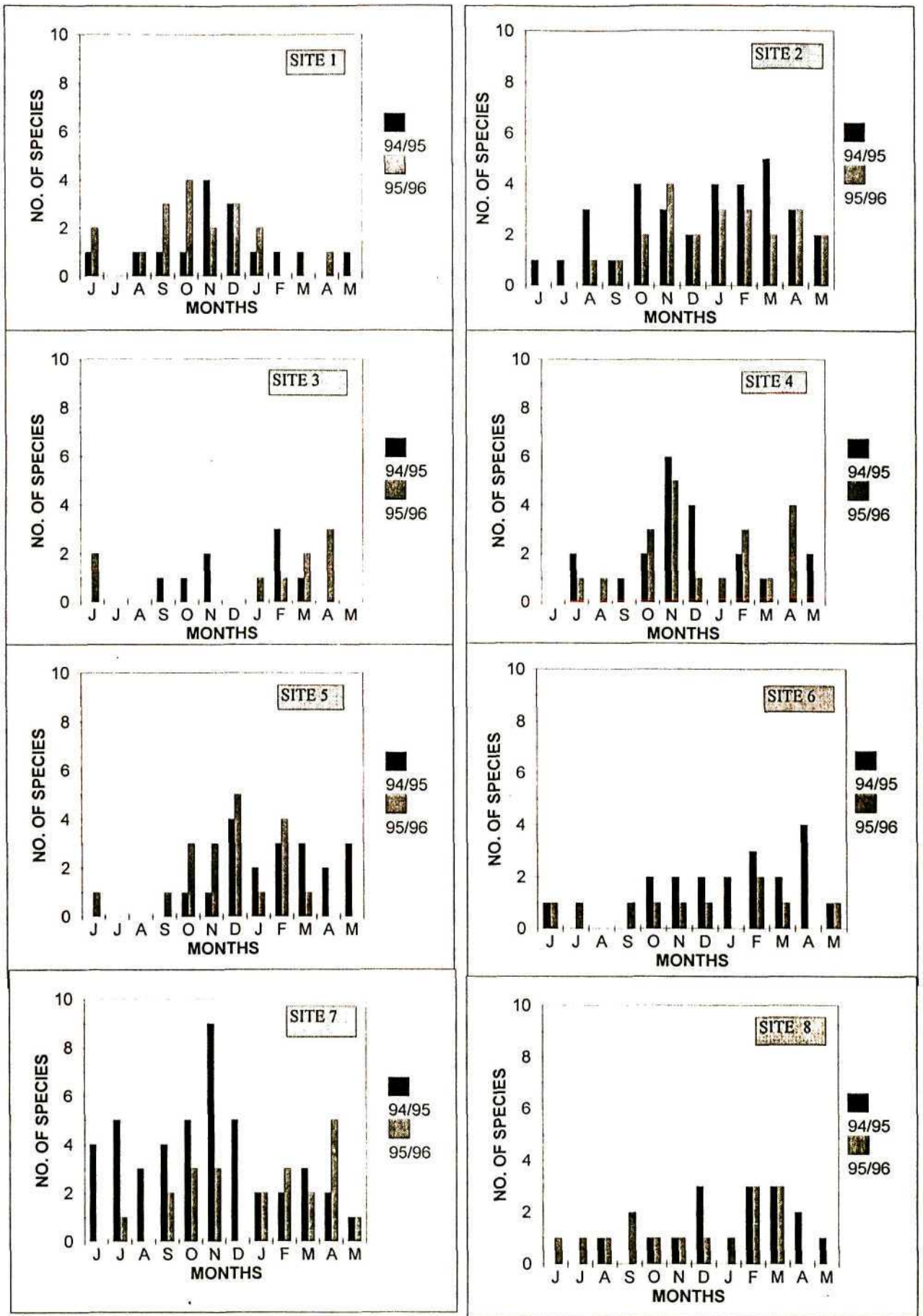


Figure 4.3(a): Number of species of carabids and cicindelids recorded over the first sampling season (June 1994 - May 1995) and the second sampling season (June 1995 - May 1996) for each of the eight sites (1-8).

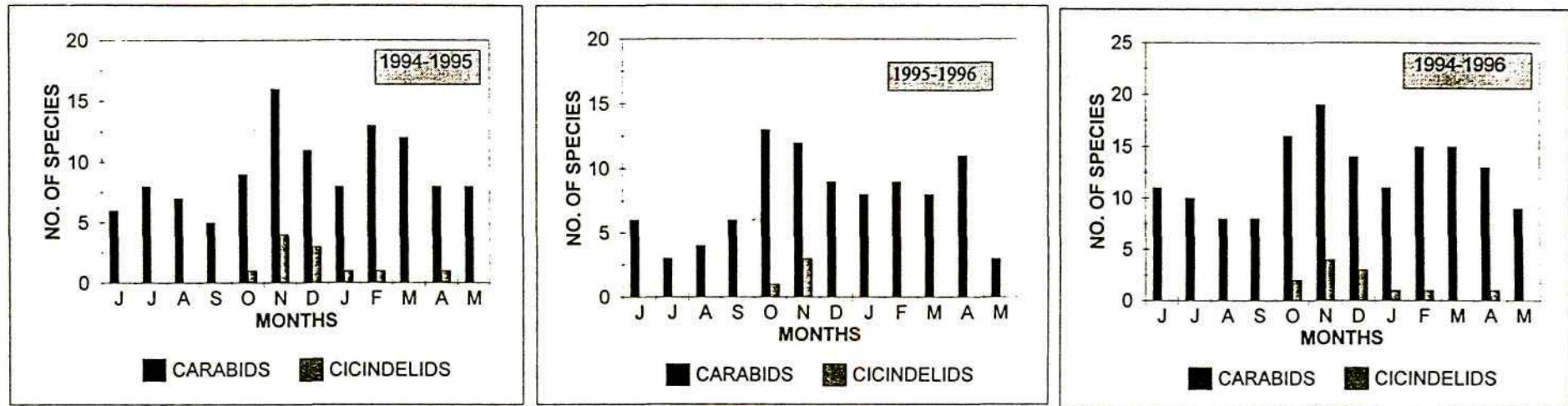


Figure 4.3(b): Proportional number of species of carabids and cicindelids recorded over the first sampling season (June 1994-May 1995), the second sampling season (June 1995-May 1996) and as the sum of the two seasons (June 1994-May 1996), arranged for each of the twelve monthly replicates, for the whole sampling area.

between abundance and number of species (Tables 4.1.2 and 4.1.2). The graphs also show that beetle species are present throughout the year. The number of species collected over each sampling season varied from one season to the next. Therefore all the possible comparisons in section 4.3.1 to 4.3.3 above as number of individuals are also true for number of species.

4.3.5 Proportionate numbers of carabids and cicindelids over time

4.3.5.1 Individuals

Fig. 4.2 (g) shows proportional abundances of carabids and cicindelids over the first sampling season, second sampling season and a sum of the two seasons. Carabid abundance was much higher than cicindelid abundance. Cicindelids made up 2.6% of the total as individuals of four species out of 35 collected. Cicindelids were present at the low-and high-altitude road verge grasslands of S4 and S6, which were subjected to autumn burning. They were recorded over summer in October, November, December, January, February and April with a peak activity between October through to January. All the four species, namely *C. inanis* (7) (was most abundant), *D. carinulata* (14), *D. gilvipes* (250a) and one undescribed Cicindelini sp. (250b), were recorded at S4. Only one species *D. gilvipes* (250a) was recorded at the other grassland road verge at S6, in the first season when the intensity of burning was higher at this site, than in the second season.

At S4, autumn burning was carried out in June, by July the ground was completely bare with no vegetation, by August the grass began to sprout and by February the grass had grown to a maximum height of about 63 cm. The grass remained long for the rest of the sampling season except for a small strip of five metres wide along electricity posts that received cutting. From Tables 4.5 and 4.14 Appendix 2, it can be seen that, the overall beetle activity peaks over the summer periods before and after burning, are the same. However, the overall abundance after burning for carabids and cicindelids together was lower than that without burning in the second season. The ratio of cicindelid to carabid individuals (56:50) was higher in the first season than in the second one (41:272). In Table 4.14 Appendix 2, it can be seen that, in the second season, cicindelids were only

recorded in the strip of cut grass within point habitat 13, together with the carabid *Graphipterus* species *G. subhamatus* (240a). These species preferred open sandy patches along the road induced by fire and cutting disturbance. Whereas *M. gilvipes* (115a) was common over the summer of both seasons, *E. caffer* (115a-w) was only recorded in the second season abundant among the tall grasses.

It appears that autumn burning management of these grasslands produces various grass successional stages that provide preferred habitats for different species. Cutting disturbance appears to also provide the same effects.

4.3.5.2 Species

Fig. 4.3(b) shows proportional number of species of carabids and cicindelids over the first sampling season, second sampling season and a sum of the two seasons.

The graphs (Fig. 4.3b) show similar patterns observed in Fig. 4.2 (g) as number of individuals over monthly samples in section 4.3.5.1 above. Therefore all comparisons under section 4.3.5.1 are equally true for number of species.

4.3.6 Population phenology in eight sites: multivariate analysis (PCA) of species abundances over time

Multivariate analysis of seasonal activity patterns of carabids allows concise information on the community activity patterns to be extracted and avoids species by species comparisons (Dufrene *et al.*, 1990). In this study carabid populations annual activity cycles in forest and grasslands, along an altitudinal gradient was compared.

In multivariate analyses of species data, CA, DCA or MDS are recommended (Ter Braak, 1988; Ludwig and Reynolds, 1988; Jongman *et al.*, 1987). The reason PCA was used in this analysis is that, CA, DCA and MDS ordinations produced diagrams with monthly sample points and species

points for individual sites (1-8), grouped at the centre of the diagrams, making it impossible to interpret the ordination. The results of both CA and DCA were found to be less than 1.5 standard deviations and it was therefore safe to use PCA (Ter Braak, 1988). PCA was carried out using data as a sum of species abundance over two sampling seasons for each site. However, it was found that, when data of the whole study area as a sum of two seasons was analysed through PCA, CA, DCA and MDS, the resulting ordination diagrams could be interpreted and they gave the same information.

Therefore the activity patterns of the total community in the eight sites (Fig. 4.3c-j) and for the whole study area (Fig. 4.3k) were analysed using PCA to represent the changes in the structure of the community with time. Sampling periods as months form a ring meaning that the first and last sampling periods are more similar than is the case when they are both compared with the middle sampling periods (Dufrene *et al.*, 1990). A perfect cycle is produced by a regular succession of species from one season to the next.

Two sampling months that are mapped closer together on the ordination diagram are characterized by a similar dominance pattern. In the same way, when two species are close, the timing of their activity patterns is similar. The changes in species abundance with time cause changes in the mean community structure represented by the position of the sampling periods. The species positions can be related to their dominance in each sampling period.

In PCA ordination diagrams, (Fig. 4.3 c-k), the axis of a species in a biplot is the (not the horizontal axis or the vertical axis) oblique axis (Ter Braak, 1988). The abundance of each species is highest over months that are situated in the vicinity of the end of the species axis. The length of each species axis is related to the fraction of the total abundance of the community, very short axis representing species with very low abundance and vice versa.

The general climate pattern per annual season in the whole study area is shown below and sampling months are represented by numbers in the ordination diagram (Fig. 4.3 c-j); June-6/July-7 (winter);

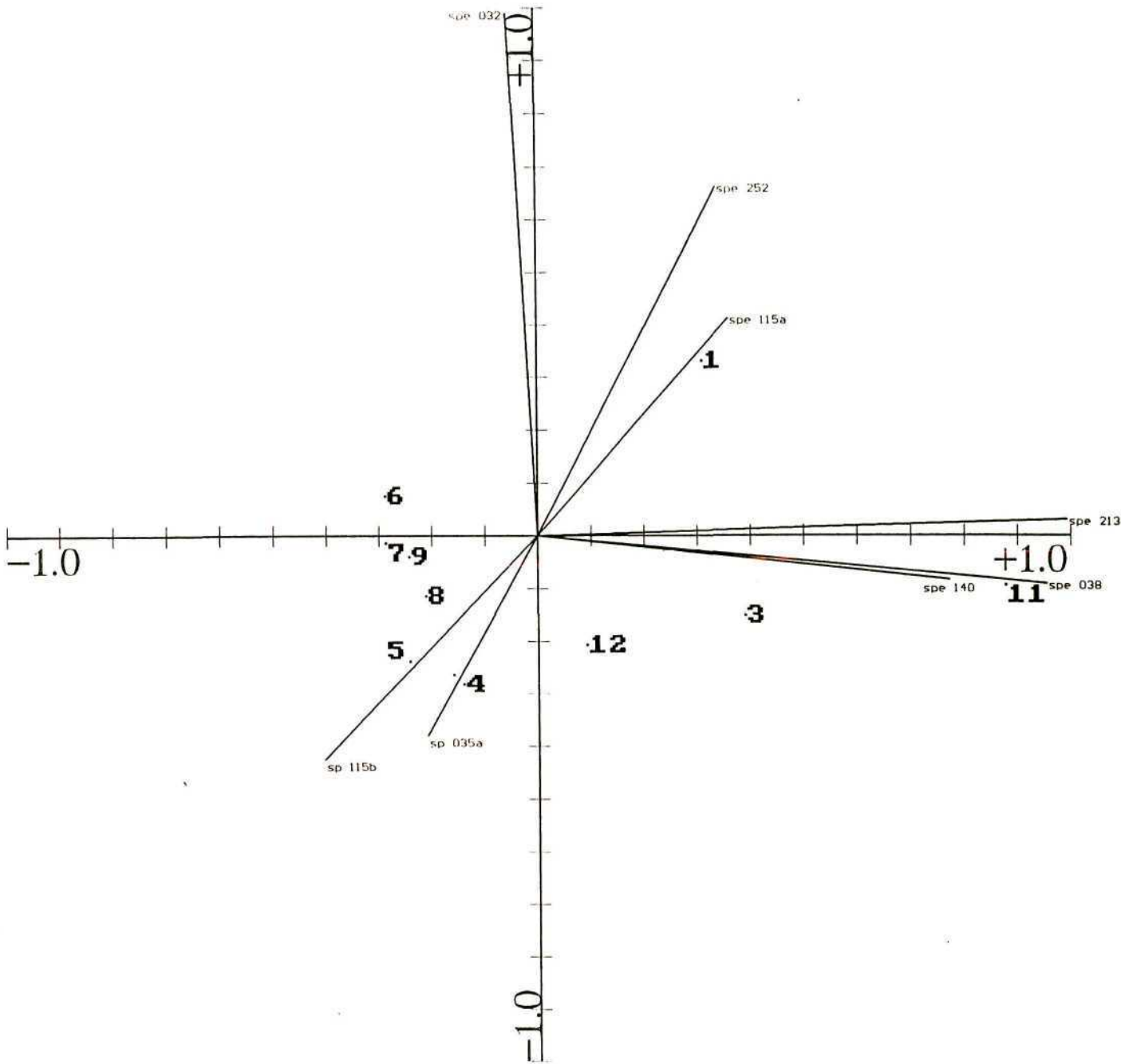


Figure 4.3 (d): PCA analysis of the succession of the sampling periods (months) throughout the year using data as sum of two years (June 1994 - May 1996), showing the occurrence of species over months in a pine plantation (Site 2). Individual species are shown by code numbers (e.g. 115a) and represented by an oblique axis (see Table 4.1 for actual species names). The numbers, 1-12 in bold type represent months in a year, e.g. January is 1 and December is 12.

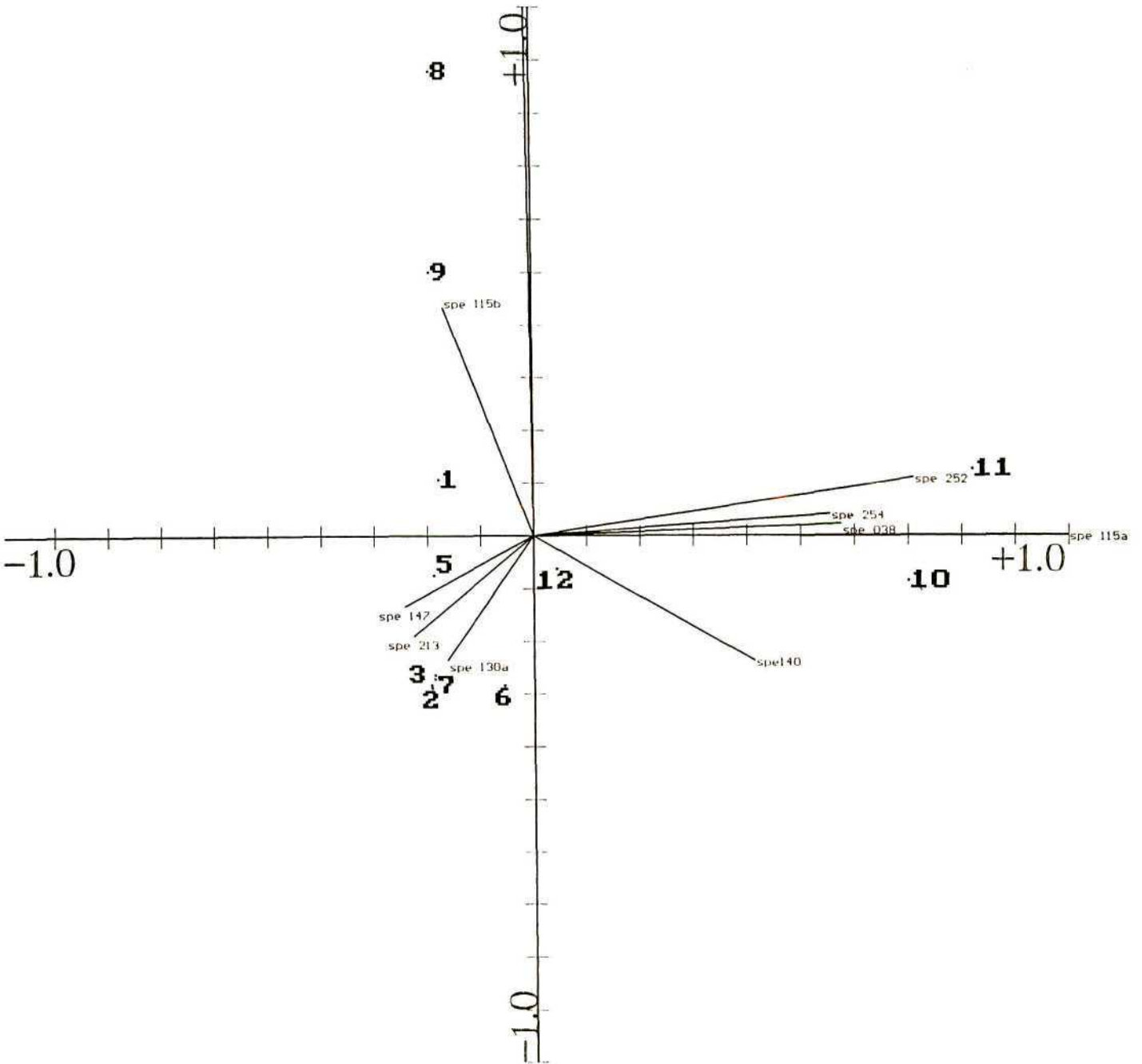


Figure 4.3 (c): PCA analysis of the succession of the sampling periods (months) throughout the year using data as sum of two years (June 1994 - May 1996), showing the occurrence of species over months in a primary indigenous forest (Site 1). Individual species are shown by code numbers (e.g. 115a) and represented by an oblique axis (see Table 4.1 for actual species names). The numbers, 1-12 in bold type represent months in a year, e.g. January is 1 and December is 12.

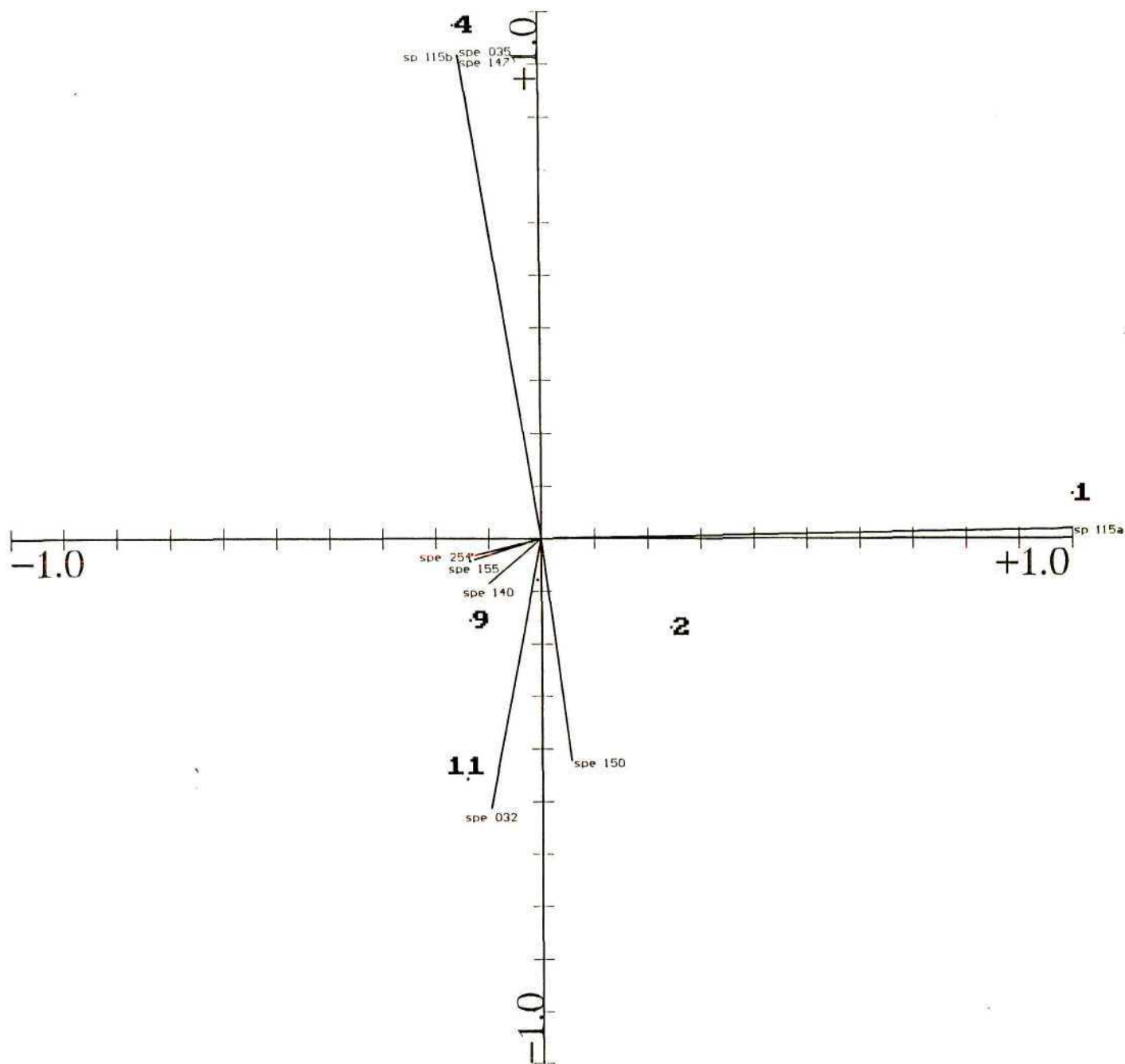


Figure 4.3 (c): PCA analysis of the succession of the sampling periods (months) throughout the year using data as sum of two years (June 1994 - May 1996), showing the occurrence of species over months in a recreational park grassland (Site 3). Individual species are shown by code numbers (e.g. 115a) and represented by an oblique axis (see Table 4.1 for actual species names). The numbers, 1-12 in bold type represent months in a year, e.g. January is 1 and December is 12.

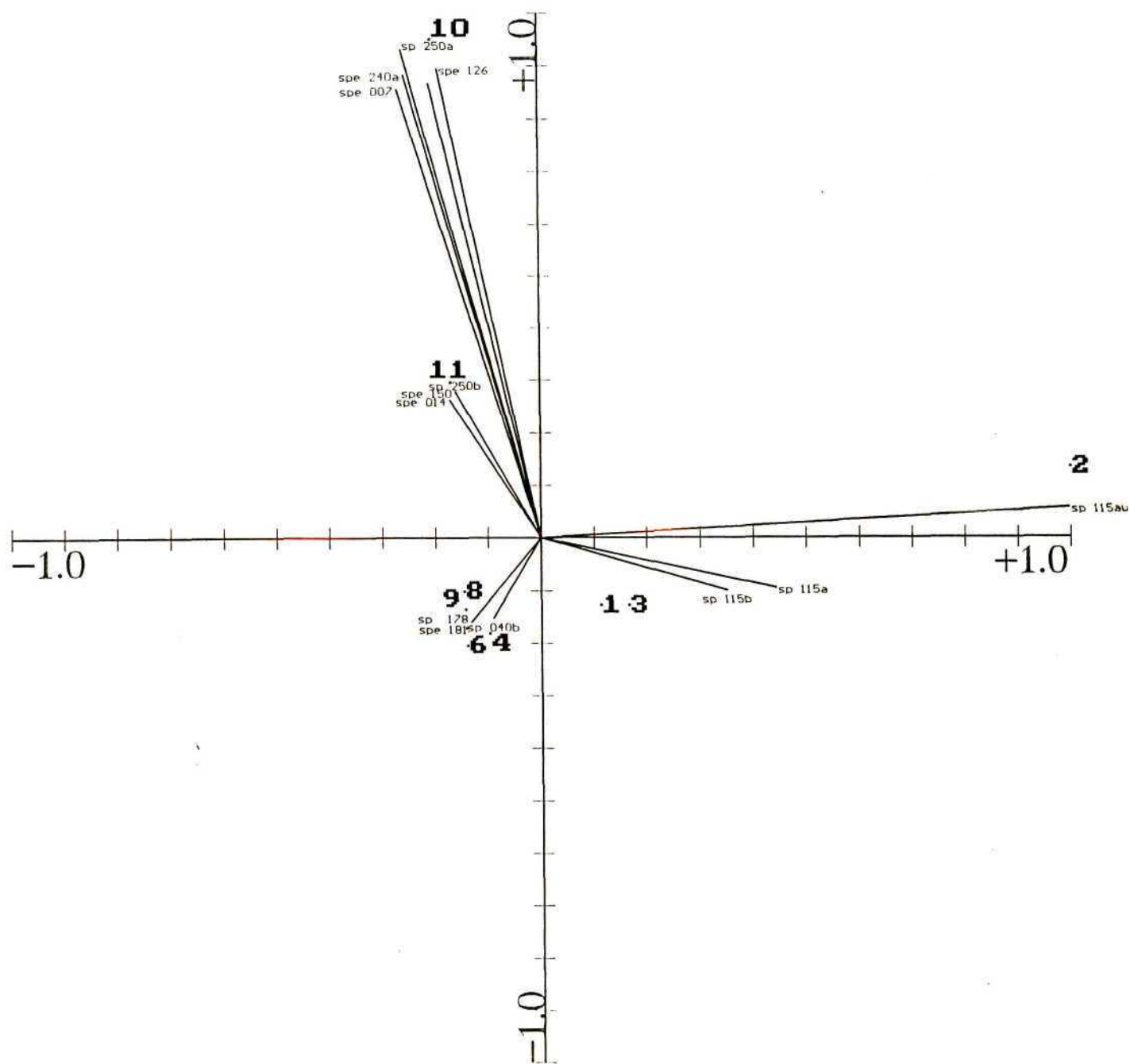


Figure 4.3 (f): PCA analysis of the succession of the sampling periods (months) throughout the year using data as sum of two years (June 1994 - May 1996), showing the occurrence of species over months in a road verge grassland at high elevation (Site 4). Individual species are shown by code numbers (e.g. 115a) and represented by an oblique axis (see Table 4.1 for actual species names). The numbers, 1-12 in bold type represent months in a year, e.g. January is 1 and December is 12.

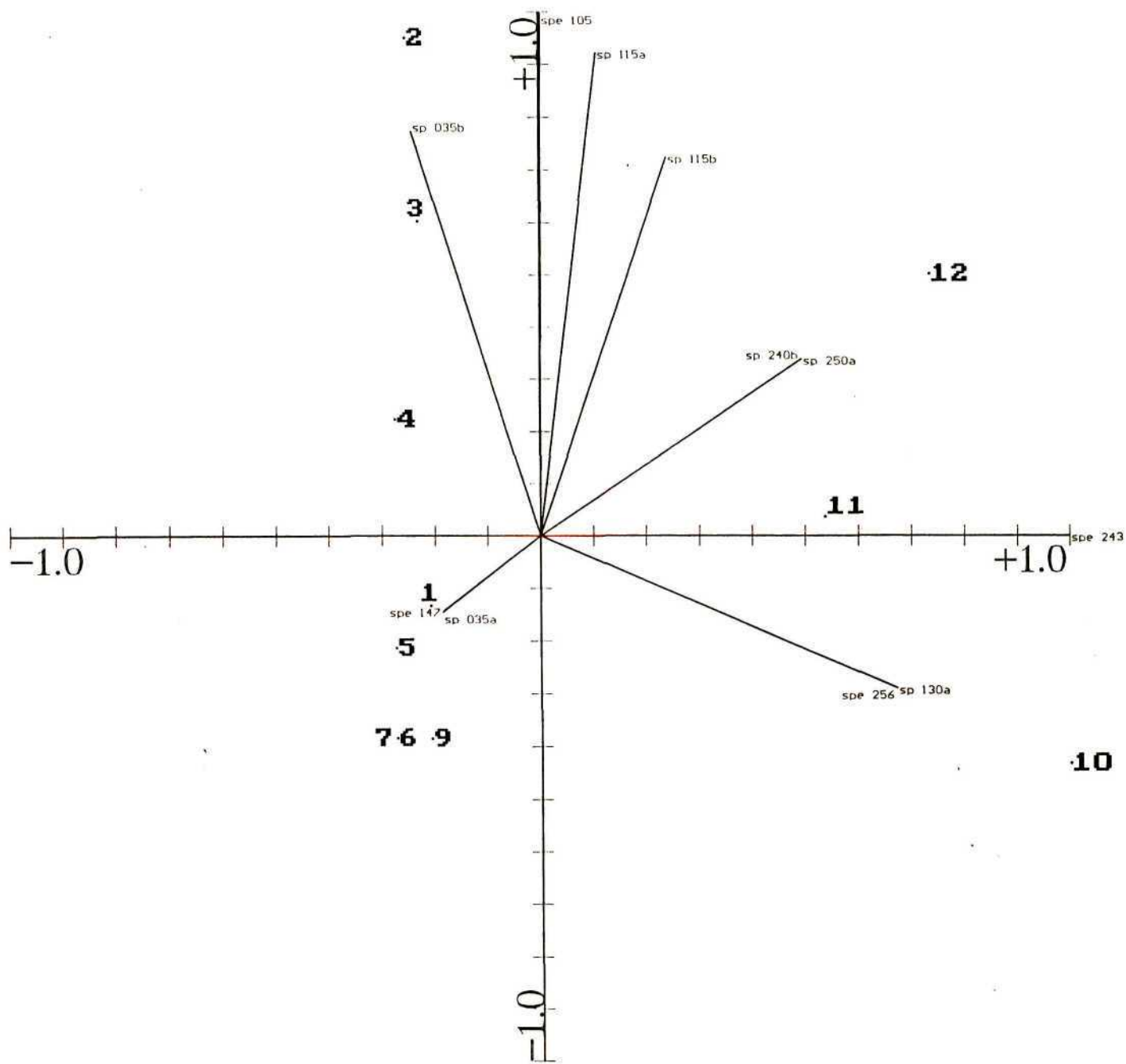


Figure 4.3 (g): PCA analysis of the succession of the sampling periods (months) throughout the year using data as sum of two years (June 1994 - May 1996), showing the occurrence of species over months in a Savanna *Acacia*-dominated woodland (Site 5). Individual species are shown by code numbers (e.g. 115a) and represented by an oblique axis (see Table 4.1 for actual species names). The numbers, 1-12 in bold type represent months in a year, e.g. January is 1 and December is 12.

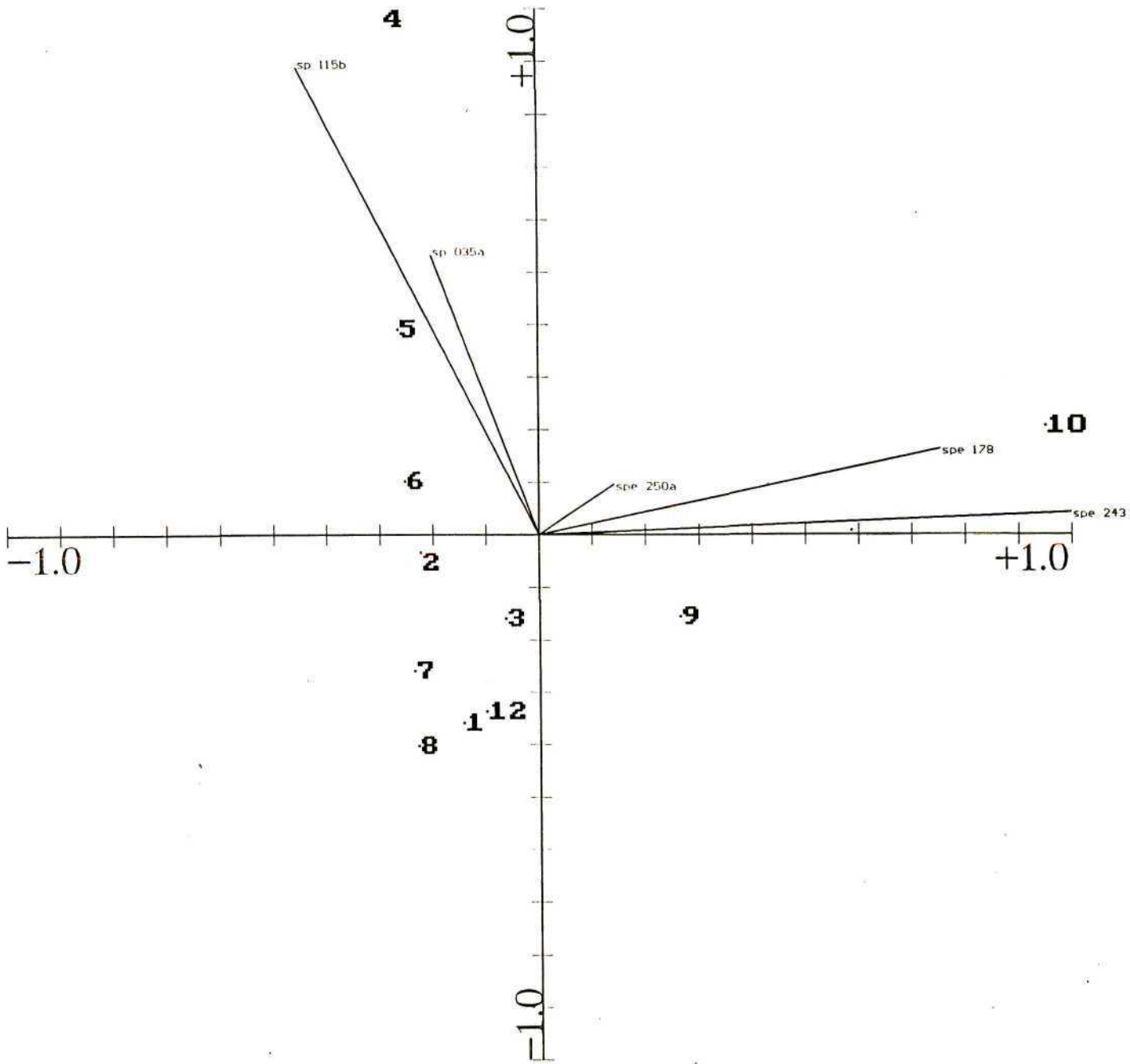


Figure 4.3 (h): PCA analysis of the succession of the sampling periods (months) throughout the year using data as sum of two years (June 1994 - May 1996), showing the occurrence of species over months in a road verge grassland at low elevation (Site 6). Individual species are shown by code numbers (e.g. 115a) and represented by an oblique axis (see Table 4.1 for actual species names). The numbers, 1-12 in bold type represent months in a year, e.g. January is 1 and December is 12.

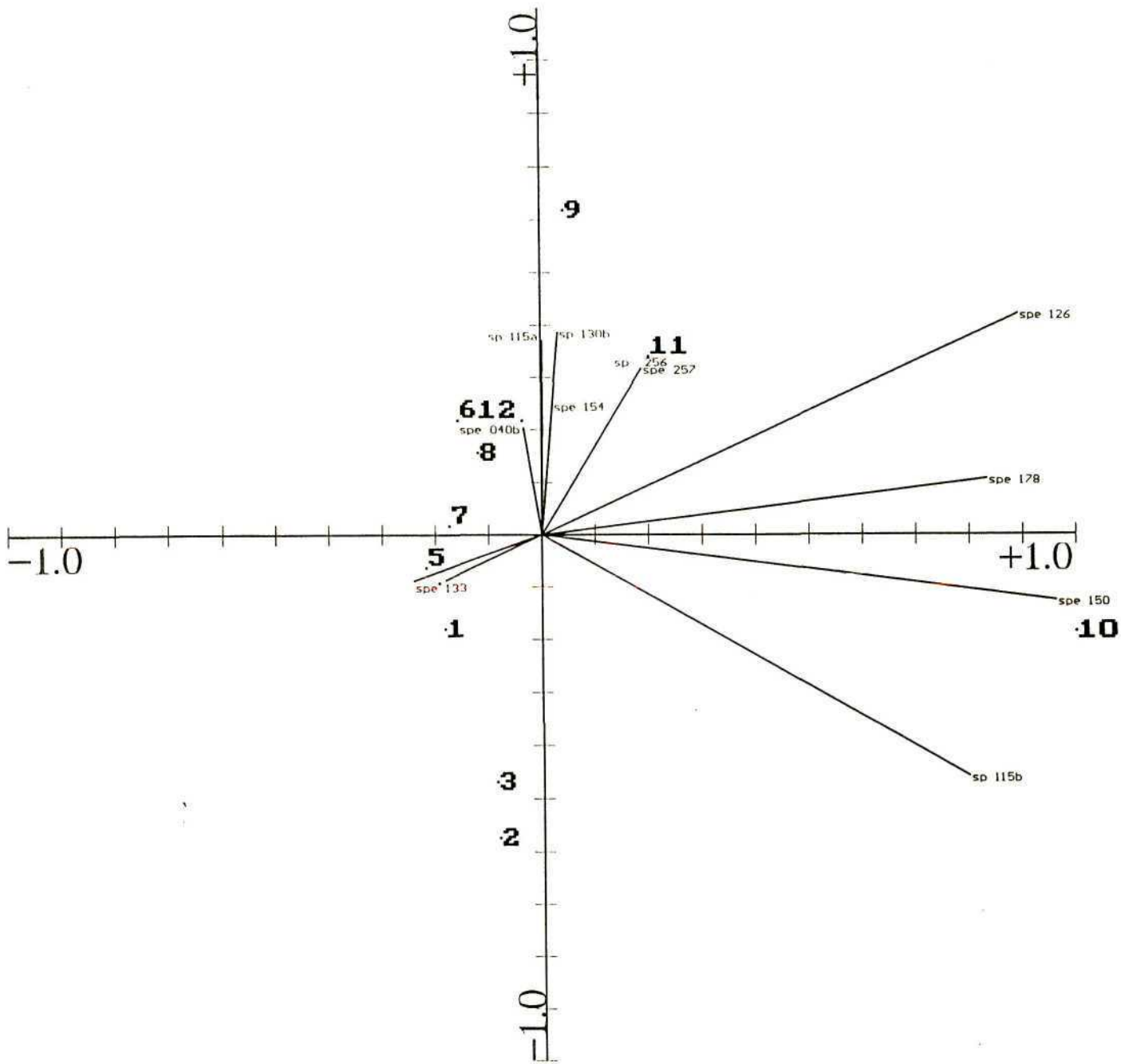


Figure 4.3 (i): PCA analysis of the succession of the sampling periods (months) throughout the year using data as sum of two years (June 1994 - May 1996), showing the occurrence of species over months in a macadamia plantation (Site 7). Individual species are shown by code numbers (e.g. 115a) and represented by an oblique axis (see Table 4.1 for actual species names). The numbers, 1-12 in bold type represent months in a year, e.g. January is 1 and December is 12.

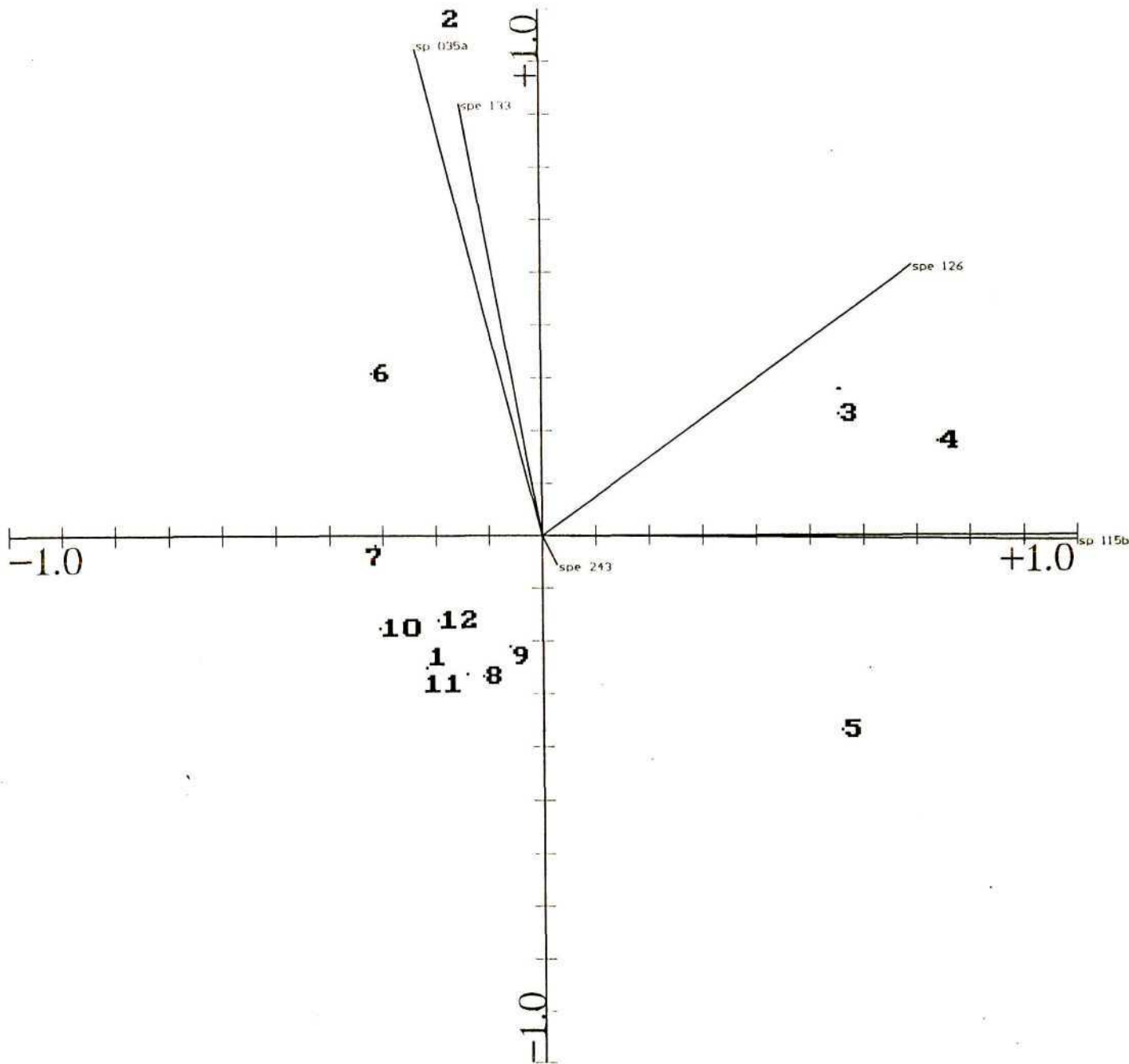


Figure 4.3 (j): PCA analysis of the succession of the sampling periods (months) throughout the year using data as sum of two years (June 1994 - May 1996), showing the occurrence of species over months in a field of hay (Site 8). Individual species are shown by code numbers (e.g. 115a) and represented by an oblique axis (see Table 4.1 for actual species names). The numbers, 1-12 in bold type represent months in a year, e.g. January is 1 and December is 12.

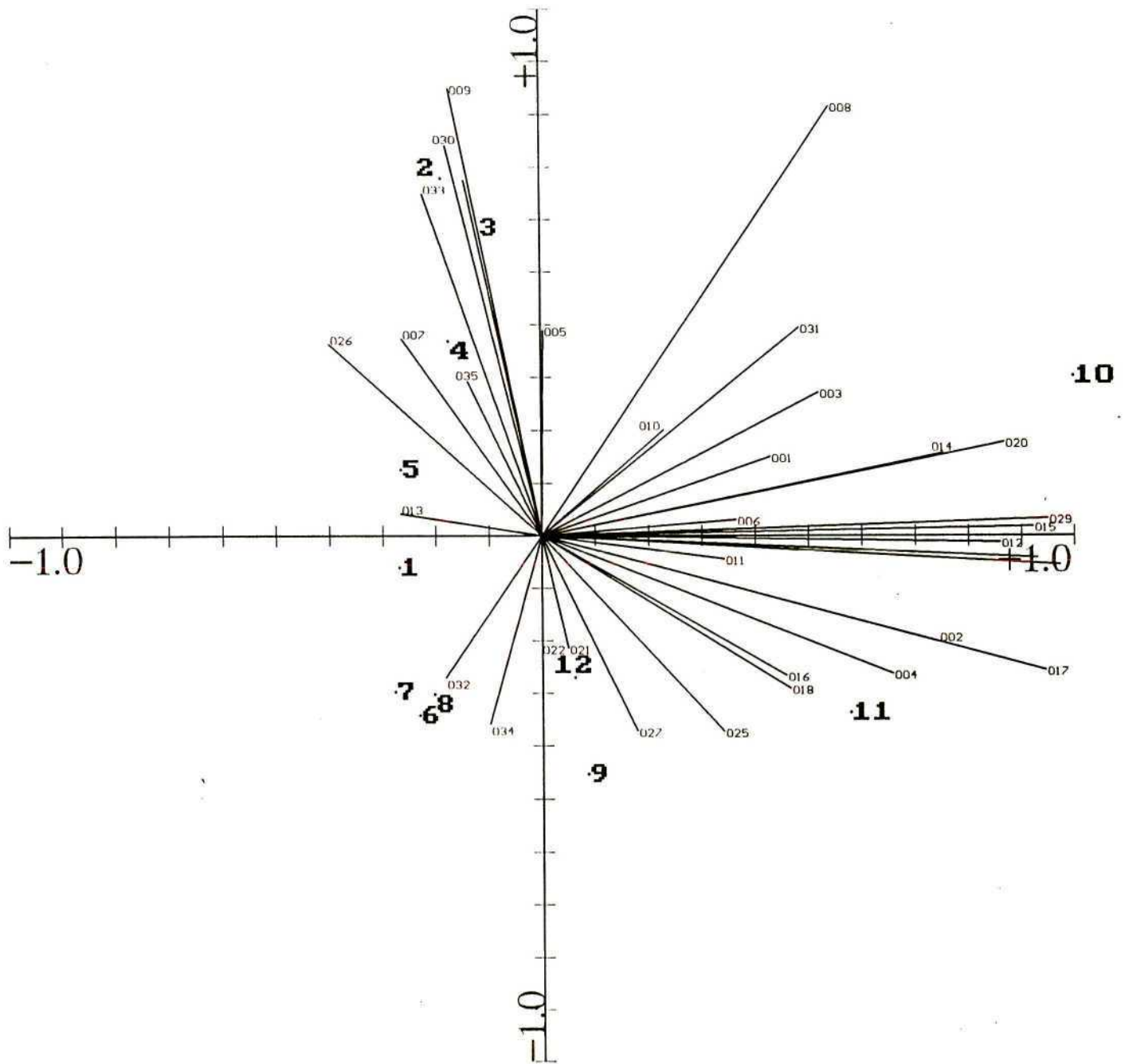


Figure 4.3 (k): PCA analysis of the succession of the sampling periods (months) throughout the year using data as sum of two years (June 1994 - May 1996), showing the occurrence of species over months in the whole study area. Species are shown as code numbers in small type following the order of listing in Table 4.20 Appendix 2, e.g. 001 is species code number 115a and represented by an oblique axis (see Table 4.1 for actual species names). The numbers, 1-12 in bold type represent months in a year, e.g. January is 1 and December is 12.

August-8/September-9 (spring); October-10, November-11, December-12 (early summer), January-1, February-1, March -3 (late summer); April-4/May-5 (autumn).

4.3.6.1 Population phenology in a natural indigenous forest (S1)

Fig. 4.3 (c) shows that at S1, most species were at their peak abundance from late spring to early summer i.e., September to January. Therefore the species shown in this region in the diagram, could be mainly late spring/early summer breeders. The highest species axis lengths were for *M. gilvipes* (115a) and *Lebiini* sp. (32) which were therefore the most dominant species. Other species were recorded in very low abundances over late summer, autumn and winter and have therefore shorter species axis lengths.

4.3.6.2 Population phenology in a pine plantation (S2)

Fig. 4.3(d) shows that at S2 most species were at their peak abundance from over summer through to autumn. Therefore this species could be mainly summer breeders. The most dominant species were *C. pseudocastellani* (38) and *Abacetus* sp. (213).

4.3.6.3 Population phenology in Acacia-dominated woodland (S5)

Fig. 4.3 (g) shows that at S5 most species were at their peak abundance throughout summer. Therefore these species could be mainly summer breeders. The most dominant species was the *Carabidae* sp. (243) which reached maximum abundance over early summer months of October and November and a smaller peak activity over late summer. There was little activity over spring and winter.

4.3.6.4 Population phenology in a macadamia plantation forest (S7)

Fig. 4.3 (i) shows that at S7, there was beetle activity from spring through to autumn with maximum

abundance over early summer (October and November). There was a period of low activity over December and January which peaked again slightly in late summer. There was very little activity over winter.

4.3.6.5 Population phenology in a road verge grassland at high altitude (S4)

Fig. 4.3 (f) shows that at S4, there were many species with high abundance over early summer mainly over October and November (e.g. cicindelid species *D. gilvipes* (250a) and *C. inanis* (007) followed by very low activity over December then rising again to reach peak activity over late summer with little activity over autumn and winter. There were some early summer breeders and late summer breeders.

4.3.6.6 Population phenology in a road verge grassland at low altitude (S6)

Fig. 4.3 (h) shows that at S6, Carabidae sp. (243) reached maximum abundance in early summer and Harpalini sp. (115b) reached maximum abundance in autumn. There was very little activity over winter.

4.3.6.7 Population phenology in a recreational park grassland (S3)

Fig. 4.3 (e) shows that at S3 the activity pattern was not very distinct. The most abundant species was *M. gilvipes* (115a), recorded from January to March with maximum abundance in January. The other species were recorded either in low abundance in a single month e.g in April and June suggesting that they may be vagrants (See Tables 4.4 and Table 4.13 Appendix 2).

4.3.6.8 Population phenology in a field grassland (S8)

Fig. 4.3 (j) shows that at S8 most species were at their peak abundance from late summer to autumn. There was very little activity over spring and early summer.

4.3.6.9 Population phenology in the whole study area

Fig. 4.3(k) shows the occurrence of species over months in the whole study area including forest and grassland. It is clear that the carabid community in this region have two peaks of activity. The first and highest starts in spring (August-8/September-9) through to early summer (October-10/November-11). Then they become dormant for a period in midsummer (December-12/January-1) and become active again in late summer (February -2 through autumn May-5), and dormant in winter (June-6, July-7).

4.4 PATTERNS OF DIVERSITY AND ABUNDANCE AMONG SITES

Tables 4.21, 4.22, 4.23 Appendix 2 illustrate number of individuals and species of carabids and cicindelids recorded over the first sampling season, second sampling season and a sum of the two seasons respectively. Fig. 4.4(a,b) compares the two seasons graphically. A total 4197 individuals of 35 species from 9 tribes were recorded over the study period (June 1994 to May 1996). The first sampling period had 2312 individuals and 29 species the second sampling period had 1885 individuals and 26 species.

4.4.1 General abundance

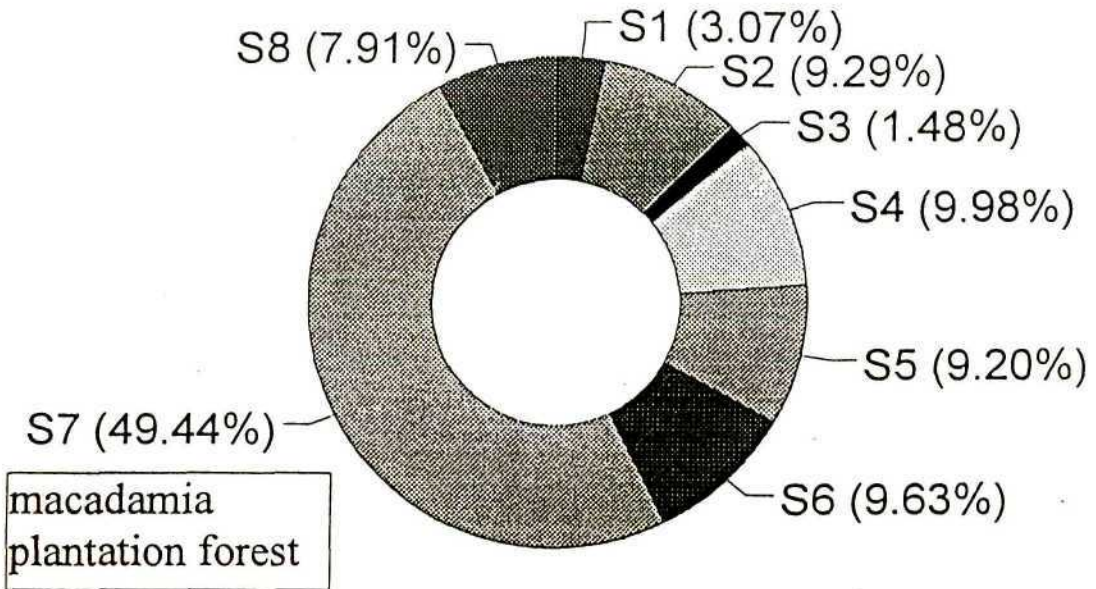
Fig. 4.4 (a) shows proportional percentages of abundance in the eight sites using data of the sum of two seasons. Order of decreasing abundance (n) given in brackets below, for each of the two sampling seasons, and the sum of the two seasons, at each of the eight sites (S1-S8), was as follows:

First season 1994/1995: S7($n=1373$), S2($n=240$), S8($n=228$), S5($n=176$), S6($n=126$), S4($n=106$), S1($n=73$), S3($n=20$).

Second season 1995/1996: S7($n=732$), S4($n=313$), S6($n=278$), S5($n=210$), S2($n=150$), S8($n=104$), S1($n=56$), S3($n=42$).

(a)

ABUNDANCE (4197) 1994-1996



(b)

SPECIES (35) 1994-1996

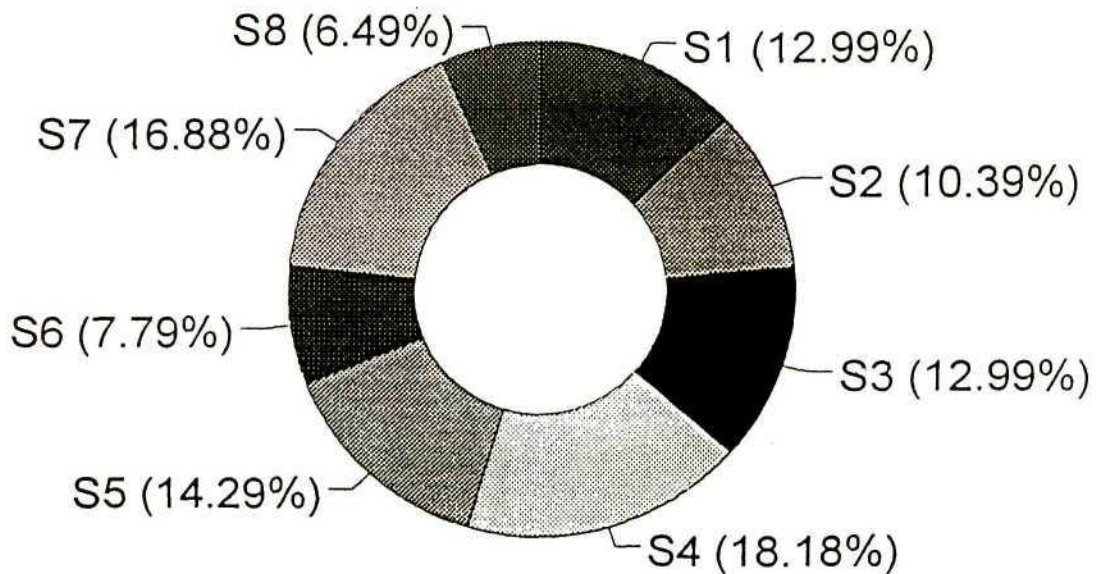


Figure 4.4: (a) Total number of individuals (4197), (b) total number of species (35), recorded over the whole study area, over two years (June 1994-May 1997), and shown proportionally for each of the eight sites (S1-S8).

Sum 1994-1996: S7($n=2075$), S4($n=419$), S6($n=404$), S2($n=390$), S5($n=386$), S8($n=332$), S1($n=129$), S3($n=62$).

The macadamia plantation (S7) had the highest beetle abundance and the park (S3) with intensive mowing of lawn had the lowest beetle abundance.

4.4.2 General species richness

Fig. 4.4 (b) shows proportional percentages of species in the eight sites using data of the sum of two seasons. Order of decreasing number of species (n) given in brackets, for each of the two sampling seasons, and the sum of the two seasons, at each of the eight sites (S1-S8), was as follows:

First season 1994/1995: S7($n=12$), S4($n=12$), S1($n=7$), S2($n=7$), S5($n=6$), S6($n=6$), S3($n=5$), S8($n=4$).

Second season 1995/1996: S4($n=9$), S1($n=8$), S5($n=8$), S2($n=7$), S3($n=7$), S7($n=6$), S6($n=3$), S8($n=3$).

Sum 1994-1996: S4($n=14$), S7($n=13$), S5($n=11$), S1($n=10$), S3($n=10$), S2($n=8$), S6($n=6$), S8($n=5$).

The number of species increases with abundance and has been shown to be highly positively correlated (Tables 4.1.1 and 4.1.2) except at the park (S3). The low abundance and high number of species at S3 can be attributed to the intensity of disturbance being frequent mowing resulting in a high species turnover in addition to influence from adjacent sites (natural indigenous forest S1 and pine plantation S2). Macadamia plantation shows a relatively low number of species (S7) compared to its total abundance (Fig. 4.4). This was due to the dominance of a few species. See section 4.3 above for species responsible for this patterns.

4.4.3 Comparison of spatial population patterns between forests and grasslands at the same altitude

4.4.3.1 Spatial population patterns in natural indigenous forest (S1) and pine plantation (S2) at high altitude

Site 2 had a higher abundance than S1 from one season to the next . There was an overall high abundance in the pine plantation with fewer number of species , whereas the natural indigenous forest (S1) had lower abundance with a higher number of species (Fig. 4.4 and section 4.4.2).

4.4.3.2 Spatial population patterns in recreational park grassland (S3) and road verge grassland (S4) at high altitude

Site 4 had a higher abundance than S3 across the two seasons. There was an overall high species abundance in the road verge grassland (S4) with autumn burning and a lower abundance at the park (S3) with frequent mowing. Therefore beetle abundance seems to be correlated to the intensity of disturbance.

4.4.3.3 Spatial population patterns in Acacia-dominated woodland (S5) and macadamia plantation (S7) at low altitude

Site 7 had a higher abundance and number of species than S5 from one season to the next. There was an overall high species abundance in the macadamia plantation over the first sampling season. However, in the second sampling season, both number of species and abundances at S7 decreased relative to S5. This may have been due to the absence of closed tree canopy at S7, in addition to the presence of open ground (without herb cover etc.) providing no shelter, and therefore the heavy rainfall over the second season affected insect populations.

4.4.3.4 Spatial population patterns in road verge grassland (S6) and field grassland (S8) at low altitude

Site 6 had a higher overall abundance and number of species than S8. It appears that autumn burning at S6 encourages more insect populations than cutting disturbance in autumn at S8. However, in the first season the intensity of burning at S6 was higher than in the second season at the same site, resulting in an overall decrease in numbers over the first season.

4.4.4 Comparison of spatial population patterns between primary and secondary forests and grasslands

4.4.4.1 Spatial population patterns in primary forests: natural indigenous forest (S1) at high altitude and a natural Acacia-dominated woodland (S5) at low altitude

The indigenous forest at high altitude (S1) had lower beetle abundance across the two sampling seasons than the *Acacia*-dominated savanna woodland (S5) at lower altitude (section 4.4.1 and Fig. 4.4a). The overall number of species was higher at S5($n=11$) than S1($n=10$). In the first season, S1 had more species ($n=7$) than S5 ($n=6$), and in the second season both sites had the same number of species ($n=8$).

4.4.4.2 Spatial population patterns in secondary forests: pine plantation (S2) at high altitude and macadamia plantation (S7) at low altitude

The pine plantation at high altitude had lower beetle abundance than the macadamia plantation at lower altitude (Fig. 4.4a and sections 4.4.1, 4.4.2). The overall number of species was higher at S7 than S2. In the first season, S7 had more species and in the second season, S2 had more species than S7.

Order of decreasing abundance over all four primary and secondary forest sites was: S7($n=2075$),

S2($n=390$), S5($n=386$), S1($n=129$). Therefore primary forest sites had lower beetle abundance than secondary sites. Sites at high altitude had lower abundance than those at low altitude. Therefore abundance appears to be affected by the intensity of disturbance and altitude.

4.4.4.3 Spatial population patterns in primary grasslands: a road verge (S4) at high altitude and a road verge (S6) at low altitude

The overall abundance at S4 was slightly higher than that at S6 (Fig. 4.4a and section 4.4.1). In the first season, S4 had lower abundance than S6 and in the second season S4 had higher abundance than S6. The overall number of species was higher at S4($n=14$) than S6($n=6$).

During the first sampling season the abundance at S4($n=104$) was lower than that at S6($n=126$). This could be a result of the intensity of disturbance at each site. S4 was burnt to bare ground at the beginning of the sampling season in June and at S6, only the area in which point habitat numbers 23 and 24 were situated burnt to bare ground and the other portion with point habitat numbers 21 and 22 remained unburnt. Therefore the level of disturbance at S4 was higher than at S6. During the second sampling season the abundance at S4($n=313$) was higher than at S6($n=278$). At S4 only a portion of five metres wide stretch under the electricity posts covering point habitat number 13 was cut to keep grass clear under the electricity posts and at S6 only grasses around point habitat numbers 21 and 22 burnt down leaving islands of grasslands around traps. Therefore the level of disturbance at S6 was higher than at S4. These observations support the importance of carrying out rotational burning (which ensures the availability of habitats) in the management of grasslands

4.4.4.4 Spatial population patterns in secondary grasslands: a recreational park (S3) at high altitude and a field (S8) at low altitude

Over the first and second sampling season, the abundance at S3, a park whose lawn was mown frequently in a year had much lower abundance ($n=62$) than S8($n=332$) a field mown once in a year (Fig.4.4a). However, the overall number of species was higher at S3 than S8 (Fig. 4.4b and section

4.4.2)

4.4 5 Proportionate numbers of carabids and cicindelids at the eight sites

During the first sampling season cicindelids were recorded at a grassland road verge S4($n=56$) situated at high altitude, S6($n=12$) a grassland road verge situated at low altitude, S5($n=2$) *Acacia*-dominated forest situated at low altitude. The proportion of cicindelid to carabid individuals was S4(56:50), S6(12:114), S5(2:174).

During the second sampling season (1995/1996), cicindelids were recorded at S4 only and the proportion of cicindelids to carabids was (41:272).

The road verge grassland (S4) was extensively burnt to bare ground at the beginning of the first sampling season in June. Fresh grass began to sprout in August, and by February, it had grown to a maximum height of about 63cm. Cicindelids were recorded in October($n=14$), November($n=42$), December($n=8$), January($n=2$), February($n=2$) and April($n=2$). The highest activity was October to December and very low activity was from January onwards. Therefore, it seems that the cicindelid species recorded do not prefer very tall grassland habitats and that burning helps to create these habitats. This finding was confirmed in the second sampling season, when in the absence of fire at S4, the whole region remained covered in very tall grass except for an area of five metres wide along the electricity posts, in which grass was cut in September covering one point habitat number 13. Cicindelids were recorded in the point habitat number 13 in October($n=23$), November($n=8$) and none were recorded in the other point habitats that had tall grasses. Visual searching also revealed high abundance of cicindelids in the cut grass region and none in the tall grass region.

In the first sampling season, the intensity of burning at the road verge grassland (S6) was lower than that at S4, this is because out of the four point habitats at S6, only two burnt to bare ground and the other two remained unburnt, and the cicindelid abundance at S6 was lower than at S4, possibly due to reduced preferred habitats at S6. In the second sampling season, all point habitats at S6 remained

unburnt and no cicindelids were recorded due to the absence of preferred habitats of short grasses.

In the *Acacia*-dominated woodland (S5), only two individuals were recorded in the first sampling season and none in the second sampling season. Site 5 was adjacent to S6, and the edge of S5 which borders S6 had burnt during autumn burning at S6, although the fire did not spread to the point habitats at S5. The two cicindelid individuals at S5 belonged to the same species, (*D. gilvipes*) that was also recorded at S6.

Carabid abundance was much higher than cicindelid abundance in the road verge grassland at S6 in both sampling seasons. However, in the road verge grassland at S4, cicindelid abundance was only higher than carabid abundance in the first season which had burning disturbance.

4.5 SPECIES DIVERSITY

Tables 4.21, 4.22, 4.23 Appendix 2 illustrates number of species of carabids and cicindelids recorded in the first sampling season, second sampling season and a sum of the two sampling seasons respectively. A total of 35 species were recorded by pitfall trapping over the whole study period. Twenty nine species were recorded over the first sampling period (June 1994- May 1995) and 26 species were recorded over the second sampling period (June 1995- May 1996).

4.5.1 Shannon's diversity H' of all eight sites

Table 4.27 gives values of Shannon's diversity H' and Fig. 4.5 graphs this information using data as a sum of two seasons. Order of decreasing diversity in the eight sites (S1-S8) using data of the sum of two seasons was:

road verge grassland at high elevation S4($H' = 1.91$), park S3($H' = 1.86$), natural indigenous forest S1($H' = 1.75$), pine plantation S2($H' = 1.55$), macadamia plantation S7($H' = 1.29$), road verge grassland at low elevation S6($H' = 0.96$), *Acacia*-woodland S5($H' = 0.89$), hay field S8($H' = 0.89$).

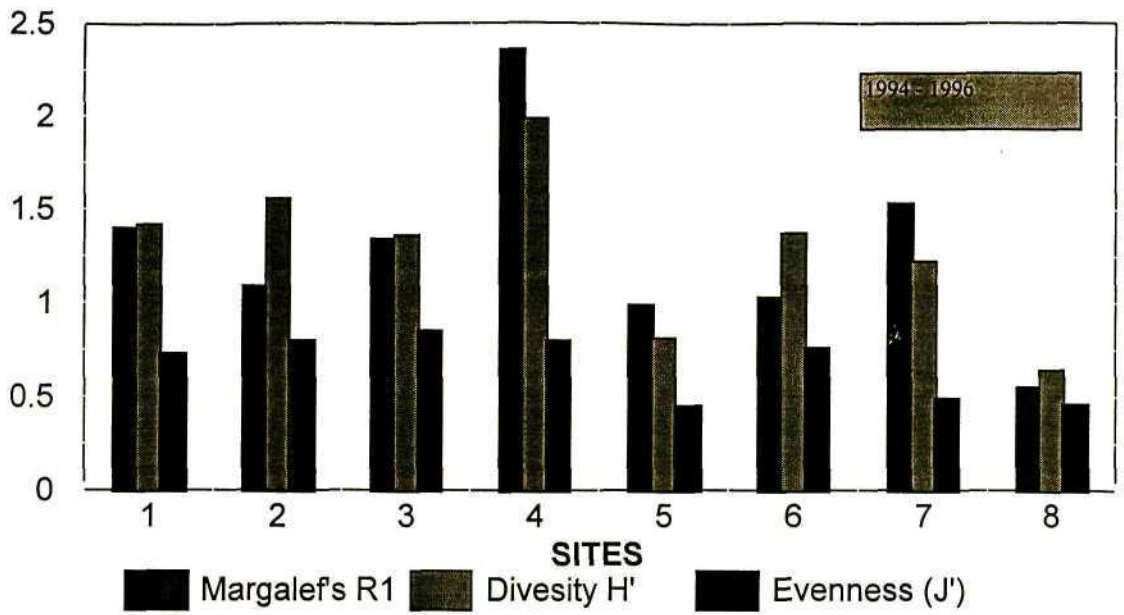


Figure. 4.5: Comparison of diversity measures of species richness (R1), Shannon's diversity index (H') and Pielou's evenness index (J'), using data as sum of the two sampling seasons (June 1994-May 1996), shown for each of the eight sites (1-8)

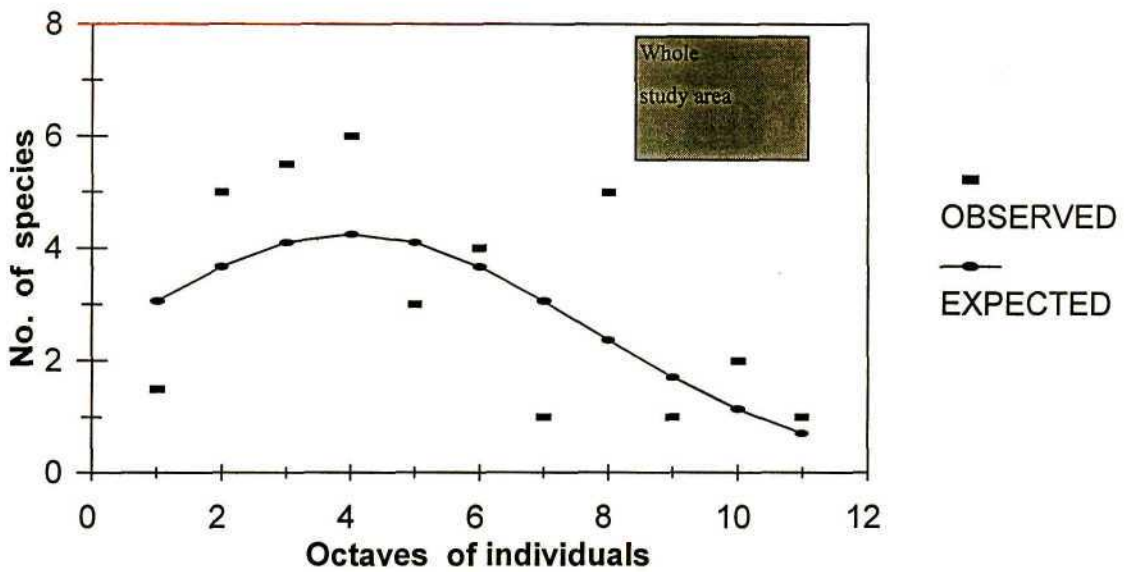


Figure 4.6(a): Frequency distribution of carabid and cicindelid abundance data, as the sum of two sampling seasons (June 1994-May 1996), plotted in octaves and shown for the whole study area. Observed data is shown as solid squares and fitted lognormal model as a curve. Octaves are classes of individuals (0-1,1-2, 2-4, 4-8, 8-16 etc). The frequency of number of individuals (n) that falls between two octaves is shared.

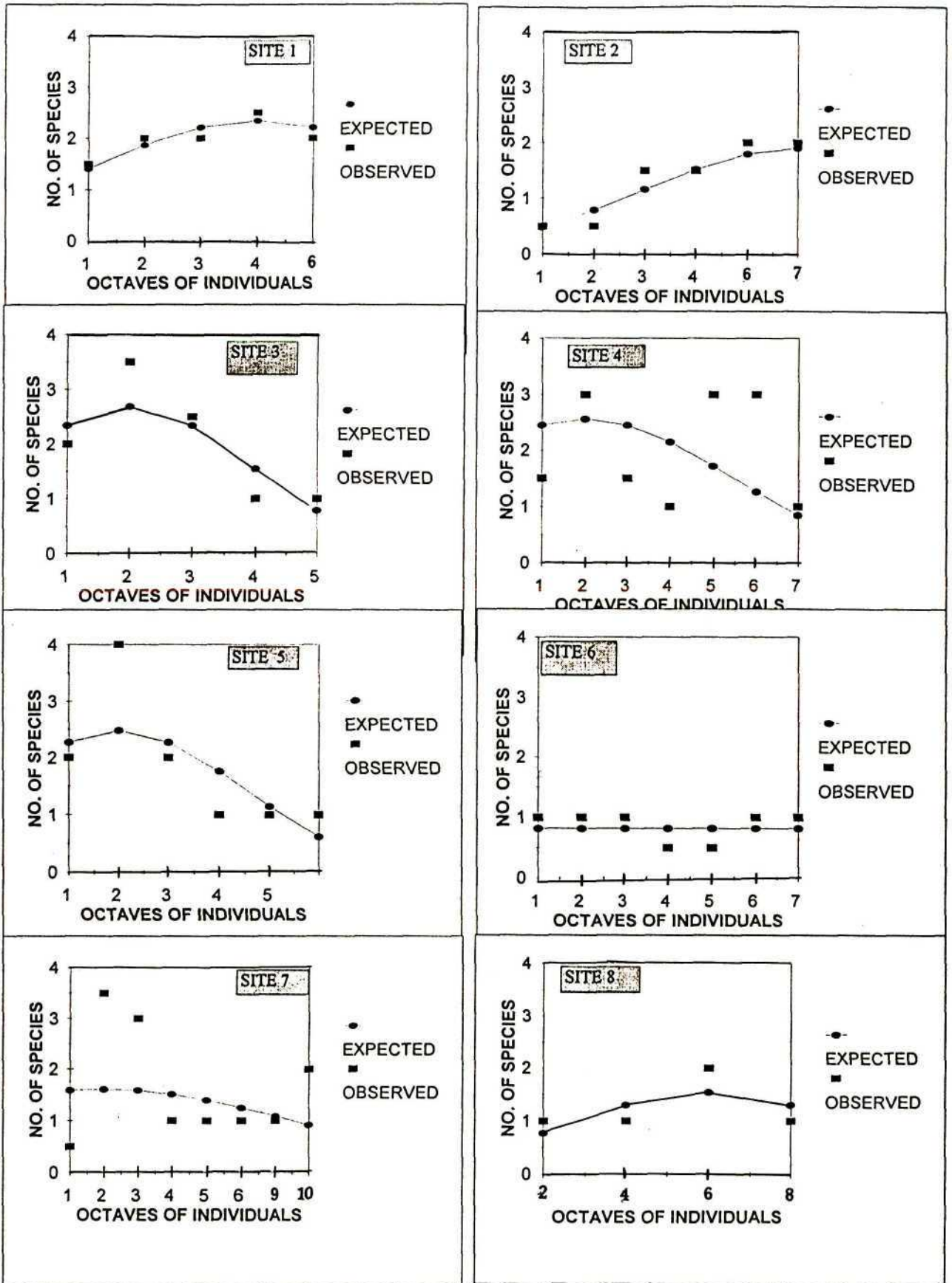


Figure 4.6(b): Frequency distribution of carabid and cicindelid abundance data, as the sum of two sampling seasons (June 1994-May 1996), plotted in octaves and shown for each of the eight sites (1-8). Observed data is shown as solid squares and fitted lognormal model as curves.

SITES	R1			H'			J'			λ			N1			N2		
	94/95	95/96	SUM	94/95	95/96	SUM	94/95	95/96	SUM	94/95	95/96	SUM	94/95	95/96	SUM	94/95	95/96	SUM
1	1.40	1.74	1.85	1.42	1.74	1.75	0.73	0.84	0.76	0.33	0.21	0.23	4.13	5.69	5.75	3.02	4.87	4.33
2	1.09	1.20	1.75	1.56	1.33	1.55	0.80	0.68	0.74	0.24	0.32	0.25	4.77	3.78	4.70	4.20	3.14	4.02
3	1.34	1.61	2.18	1.36	1.40	1.86	0.85	0.72	0.81	0.28	0.35	0.22	3.89	4.06	6.41	3.52	2.86	4.65
4	2.36	1.39	2.15	1.99	1.49	1.91	0.80	0.68	0.72	0.17	0.33	0.22	7.35	4.45	6.74	6.02	3.02	4.64
5	0.99	1.31	1.68	0.81	0.87	0.89	0.45	0.42	0.37	0.60	0.63	0.62	2.24	2.38	2.42	1.66	1.58	1.62
6	1.03	0.36	0.83	1.37	0.49	0.96	0.76	0.45	0.53	0.30	0.75	0.50	3.93	1.64	2.60	3.37	1.34	2.01
7	1.53	0.76	1.57	1.22	1.15	1.29	0.49	0.64	0.50	0.40	0.37	0.34	3.40	3.14	3.62	2.49	2.72	2.97
8	0.55	0.43	0.70	0.64	0.95	0.89	0.46	0.86	0.55	0.67	0.42	0.55	1.90	2.58	2.43	1.50	2.40	1.83

Table 4.27: Diversity indices of the eight sites, over the first sampling season (1994/1995), second sampling season (1995/1996) and sum of the two seasons (1994-1996). Margalef's index (R1), Shannon's index (H'), Pielou's evenness index (J'), Simpson's index (λ), Hill's diversity numbers (N1) and (N2).

Point habitats	R1			H'			J'			λ			N1			N2			
	1st	2nd	Sum	1st	2nd	Sum	1st	2nd	Sum	1st	2nd	Sum	1st	2nd	Sum	1st	2nd	Sum	
S 1	1	1.21	1.89	2.15	1.33	1.75	1.99	0.96	0.98	0.96	0.21	0.12	0.11	3.78	5.74	7.33	4.71	8.27	8.78
	2	0.96	0.72	1.21	1.04	0.89	1.33	0.95	1.00	0.96	0.29	0.33	0.21	2.83	2.00	3.78	3.50	3.00	4.71
	3	0.81	0.59	0.70	0.70	1.06	1.10	0.50	0.97	0.79	0.65	0.34	0.40	2.00	2.89	2.98	1.30	2.96	2.51
	4	0.80	1.44	1.67	0.87	1.39	1.61	0.79	1.00	0.90	0.45	0.14	0.20	2.38	4.00	5.00	2.20	7.00	5.00
S 2	5	1.18	0.65	1.33	1.18	0.86	1.29	0.66	0.78	0.86	0.39	0.46	0.39	3.27	2.36	3.64	2.54	2.16	2.58
	6	1.14	0.60	1.07	1.40	1.06	1.42	0.78	0.97	0.79	0.28	0.33	0.28	4.05	2.89	4.14	3.64	3.00	3.62
	7	0.00	0.80	1.05	0.00	1.09	1.26	1.70	0.79	0.78	1.00	0.37	0.32	1.00	2.97	3.53	1.00	2.72	3.09
	8	0.67	1.23	1.00	1.30	1.20	1.35	0.94	0.67	0.75	0.28	0.42	0.32	3.66	3.32	3.84	3.52	2.40	3.17
S 3	9	0.00	0.72	0.72	0.00	0.69	0.69	0.00	1.00	1.00	0.00	0.33	0.33	0.00	2.00	2.00	0.00	3.00	3.00
	10	0.40	0.72	1.08	0.64	0.69	1.21	0.92	1.00	0.88	0.52	0.33	0.30	1.89	2.00	3.36	1.94	3.00	3.33
	11	0.00	0.92	1.20	0.00	0.79	0.99	1.70	0.57	0.62	1.00	0.59	0.51	1.00	2.21	2.70	1.00	1.68	1.95
	12	1.12	0.48	1.52	1.10	0.69	1.55	1.00	1.00	0.96	0.20	0.43	0.16	3.00	2.00	4.71	5.00	2.33	6.07
S 4	13	1.57	1.02	1.38	1.58	1.36	1.61	0.88	0.76	0.77	0.22	0.29	0.23	4.87	3.91	5.00	4.60	3.51	4.28
	14	0.63	0.74	1.14	0.96	0.71	1.32	0.87	0.51	0.74	0.41	0.63	0.35	2.61	2.02	3.73	2.46	1.58	2.83
	15	1.80	0.54	1.99	1.67	0.98	1.77	0.93	0.89	0.81	0.17	0.40	0.22	5.30	2.65	5.88	6.00	2.50	4.64
	16	2.41	0.90	2.27	2.10	0.98	1.79	0.91	0.61	0.72	0.12	0.46	0.24	8.13	2.66	6.00	8.20	2.17	4.10
S 5	17	0.54	1.18	0.94	1.05	1.51	1.34	0.96	0.94	0.83	0.34	0.21	0.28	2.87	4.51	3.81	2.91	4.78	3.56
	18	1.13	0.44	1.03	0.87	0.28	0.51	0.54	0.25	0.28	0.59	0.88	0.79	2.39	1.32	1.66	1.71	1.14	1.26
	19	0.00	0.87	0.52	0.00	0.95	0.36	1.70	0.87	0.32	1.00	0.38	0.83	1.00	2.59	1.43	1.00	2.65	1.20
	20	0.48	0.69	0.81	0.50	0.60	0.59	0.46	0.42	0.37	0.73	0.72	0.72	1.65	1.81	1.81	1.37	1.40	1.38
S 6	21	0.77	0.63	0.93	0.86	1.01	1.00	0.62	0.92	0.62	0.51	0.36	0.46	2.37	2.75	2.72	1.95	2.78	2.19
	22	0.61	0.29	0.75	0.54	0.69	0.88	0.49	1.00	0.64	0.72	0.49	0.49	1.71	2.00	2.41	1.39	2.06	2.05
	23	0.57	0.22	0.61	0.68	0.10	0.34	0.62	1.44	0.25	0.81	0.96	0.86	1.97	1.00	1.41	1.65	1.04	1.17
	24	0.72	0.21	0.61	0.97	0.14	0.42	0.89	0.20	0.30	0.37	0.94	0.82	2.65	1.15	1.52	2.73	1.07	1.23
S 7	25	1.64	0.71	1.57	1.54	0.96	1.54	0.67	0.89	0.87	0.30	0.44	0.30	4.64	2.82	4.66	3.37	2.29	3.33
	26	0.78	0.44	0.76	0.92	0.87	0.97	0.51	0.81	0.54	0.52	0.46	0.47	2.51	2.42	2.64	1.93	2.16	2.72
	27	0.66	0.80	0.88	0.87	1.14	1.12	0.54	0.64	0.58	0.51	0.37	0.37	2.38	3.12	3.06	1.95	2.67	2.70
	28	1.21	0.24	1.03	1.46	0.19	1.04	0.81	0.27	0.56	0.27	0.91	0.51	4.29	1.20	2.83	3.68	1.10	1.97
S 8	29	0.41	0.48	0.57	0.45	0.81	0.76	0.41	0.73	0.55	0.78	0.47	0.61	1.56	2.24	2.14	1.28	2.14	1.65
	30	0.69	0.00	1.00	0.87	0.00	1.11	0.79	1.70	0.80	0.47	1.00	0.38	2.38	1.00	3.02	2.13	1.00	2.60
	31	0.66	0.57	0.75	0.80	0.96	1.01	0.73	0.87	0.73	0.53	0.42	0.45	2.22	2.61	2.75	1.89	2.41	2.22
	32	0.24	0.72	0.24	0.60	0.69	0.61	0.86	1.00	0.86	0.59	0.33	0.58	1.82	2.00	1.84	1.71	3.00	1.74

Table 4.28: Diversity indices of the 32 point habitats of the eight sites (S1-S8), over the first (1st) sampling season (1994/1995), second (2nd) sampling season (1995/1996) and sum of the two seasons (1994-1996). Margalef's index (R1), Shannon's index (H'), Pielou's evenness index (J'), Simpson's index (λ), Hill's diversity numbers (N1) and (N2).

The road verge grassland at high altitude with autumn burning disturbance had the highest diversity and a field of hay mown once in autumn had the least diversity. Order of decreasing diversity shows that, the first four sites situated at high altitude have higher diversity than the last four sites situated at low altitude.

Order of decreasing diversity H' of the eight sites (S1-S8) using data of individual seasons was:

First season (1994/1995): road verge grassland at high elevation S4($H' = 1.99$), pine plantation S2($H' = 1.56$), natural indigenous forest S1($H' = 1.42$), road verge grassland at low elevation S6($H' = 1.37$), park S3($H' = 1.36$), macadamia plantation S7($H' = 1.22$), *Acacia*-woodland S5($H' = 1.81$), hay field S8($H' = 0.64$).

Second season (1995/1996): natural indigenous forest S1($H' = 1.74$), road verge grassland at high elevation S4($H' = 1.49$), park S3($H' = 1.40$), pine plantation S2($H' = 1.33$), macadamia plantation S7($H' = 1.15$), hay field S8($H' = 0.95$), *Acacia*-woodland S5($H' = 0.87$), road verge grassland at low elevation S6($H' = 0.49$).

It is clear that diversity across seasons within sites varied but not dramatically. The only major changes observed in diversity were at road verge grassland at high elevation S4 and S6, which are grasslands subjected to autumn burning in the first season, and had higher diversity than during the second season when sites were either unburnt (S4) or when the burning intensity was reduced (S6). Therefore, factors affecting diversity appear to be intensity of disturbance, altitude, year to year variation.

4.5.1.1 Shannon's diversity (H') in forests and grasslands at high altitude

The disturbed grassland habitats, road verge S4($H' = 1.91$) and park S3($H' = 1.86$) had higher diversity than the forest habitats, natural indigenous forest S1($H' = 1.75$) and pine plantation S2($H' = 1.55$). Site 4 had been burnt completely at the beginning of the first season, had the highest

diversity, followed by park S3 whose lawn was mown at least six times in the year. In forest habitats, the pine plantation (S2) in middle successional stage, pruned once in October over the first season had lower diversity than the natural indigenous forest (S1) with no anthropogenic disturbance.

4.5.1.2 Shannon's diversity(H') in forests and grasslands at low altitude

The macadamia plantation S7($H'= 1.29$) with agricultural management had a higher diversity than the *Acacia*-dominated woodland S5($H'= 0.89$). Overall, the road verge grassland S6($H'= 0.96$) with burning disturbance had higher diversity than a grassland field mown for hay once a year hay field S8($H'= 0.89$). However, the diversity at S6 dropped over the second season due to increased intensity of burning in addition to flooding. At low altitude, disturbed grasslands have higher diversity than forest habitats. Macadamia plantation is under intensive irrigation management which may be the result of its high diversity. Therefore, macadamia plantation S7 and road verge grassland at low elevation S6 experienced higher levels of anthropogenic disturbance namely intensive agricultural management and burning respectively, had higher diversity than *Acacia*-woodland S5 and hay field S8 with minimum disturbance, namely nature management and cutting once in a year.

4.5.1.3 Shannon's diversity H' in primary and secondary forests

Order of decreasing diversity H' of all forest sites was: natural indigenous forest S1 ($H'= 1.75$), pine plantation S2($H'= 1.55$), macadamia plantation S7($H'= 1.29$), *Acacia*-woodland S5($H'= 0.89$).

In primary forests, the natural indigenous forest (S1) at high altitude had higher diversity than the *Acacia*-dominated woodland (S5) at low altitude. In secondary forests, pine plantation (S2) at high altitude had higher diversity than macadamia plantation (S7) under agricultural management. Therefore, factors such as vegetation type and altitude affect diversity and nature of forest as primary or secondary appears to have no influence

4.5.1.4 Shannon's diversity H' in primary and secondary grassland

Order of decreasing diversity of all grassland sites was: road verge grassland at high elevation S4($H' = 1.91$), park S3($H' = 1.86$), road verge grassland at low elevation S6($H' = 0.96$), hay field S8($H' = 0.89$). Grasslands at high altitude (S4, S3) had higher diversity than those at low altitude (S6, S8).

In primary grasslands, a road verge (S4) at high altitude with autumn burning disturbance had higher diversity than S6 at low altitude with autumn burning. In secondary grasslands, a recreational park (S3) at high altitude with intensive mowing of lawn had higher diversity than hay field S8 at low altitude with lawn mown once in a year. It appears that, both altitude and the intensity of disturbance at a site influences diversity.

4.5.2 Species richness Margalef's $R1$, Shannon's diversity H' and Pielou's evenness J' in the eight sites.

Table 4.27 gives values of diversity measures. Fig. 4.5 (a) graphs these indices using data of the sum of two seasons (1994-1996) at each of the eight sites. It can be seen that diversity (H') and Margalef's species richness ($R1$) and Pielou's evenness index (J') varied from one season to the next season within individual sites and among sites. It is also clear that forests and grassland sites at high altitude with an Escarpment climate and high rainfall (S1, S2, S3, S4) had higher species richness, diversity and evenness than those at low altitude with a Savanna climate and low rainfall. Results of species richness and evenness show similar patterns like those of diversity in section 4.5.1-4.5.1.4.2 above.

Overall grassland sites S3 and S4 at high altitude had high species richness, diversity and evenness and an *Acacia*-dominated woodland (S5) at low altitude had the lowest evenness. This low evenness,

(evenness being the opposite of dominance) was the result of a single Carabidae sp. (243) with 77% dominance at S5.

4.5.3 Diversity measures in point habitats at each of the eight sites

Tables 4.24, 4.25, 4.26 Appendix 2 shows number of species of carabids and cicindelids recorded at point habitats over the first sampling season, second sampling season and the sum of the two sampling seasons respectively. Table 4.28 gives values of Shannon's diversity H' and other diversity indices of the 32 point habitats.

From these tables, it can be seen that there is variation in diversity measures from one season to the next in all the eight sites and it changes from point habitat to point habitat within a site (see also Tables 4.2 - 4.18), such that in some sites, certain point habitats have a marked higher or lower diversity than others. For instance, in the park (S3), more species were caught at point habitat numbers 10, 11 and 12 than at point habitat number 9, hence the low diversity at point habitat 9 (Table 4.28). Many species were present at point habitat 11 and 12 which were situated in the vicinity of trees providing shade and leaf litter and point habitat 10 which was situated near stones, both of these conditions seem to provide preferred habitats for carabids. On the other hand point habitat number 9 was situated in the open with no shade leaf litter or stones and no carabids were recorded over the first season and only two species of four individuals were recorded over the second sampling period.

In the *Acacia*-dominated woodland (S5), point habitat number 17 had the highest diversity, may be as a result of its nearness to a river. Whereas, the Carabidae sp. (243) was the most dominant at this S5, and it reached maximum abundance at point habitat number 18, hence the lower diversity and evenness relative to point habitat 17 (Table 4.28).

In the macadamia plantation (S7), there were many dominant Harpalini species which were found almost at all the point habitats. This is supported by the near similar diversity and evenness values

in the four point habitats at this site (Tables 4.28, 4.8, 4.17).

In the pine plantation (S2), the dominant *Abacetus* sp. (213) and *C. pseudocastellani* (38) were found in almost all the point habitats in near equal numbers and hence the evenness index in the four point habitats at this site was almost equal in value (Table 4.28).

4.5.4 Proportion of carabids and cicindelid species in point habitats of the eight sites

Cicindelid species were recorded only at S4, S6 and S5. At S4, cicindelids were recorded at all four point habitats during the first sampling season after autumn burning. In the second season cicindelids were only recorded at point habitat number 13 where grass was cut indicating that the cicindelid species caught preferred short grass. In the first season, proportion of cicindelids to carabids as number of species was (4:2) respectively. In the second season the proportion was equal (3:3).

In the road verge grassland (S6), after autumn burning in the first season, only one cicindelid species *D. gilvipes* was recorded. During the second season, when point habitats remained unburnt, there were no cicindelids recorded.

In the *Acacia*-dominated woodland (S5), one cicindelid species was recorded at point habitat number 18 which was adjacent to the border of S6. This was the same species which had been recorded at S6.

4.5.5 Rarefaction model for species richness

This analysis was carried out to confirm results of Margalef's species richness index (R1) in the eight sites (section 4.5.2). The best measure of species richness is to make direct counts of species numbers in samples of equal size (Ludwig and Reynolds, 1988). However, sample sizes are usually not equal. The method of rarefaction was used to help overcome the incompatibility of unequal

sample sizes from various communities. The method calculates the numbers of species expected from different communities if all samples are reduced to a standard size. Table 4.31a gives values of probabilities of the expected number of species $E(S_n)$ obtained from running the computer program RAREFRAC.BAS (Ludwig and Reynolds, 1988). Due to a small sample size at Site 3, species richness using data of individual seasons and of the sum of the two seasons were compared at three standard sample sizes $n=5$, $n=15$ and $n=35$ respectively. Table 4.31(b) shows the eight sites in order of decreasing species richness.

Looking at the results using data of the two seasons and at $n=5$ in Table 4.31b, only two groups of decreasing species richness are distinguished. At $n=15$ and $n=35$ only five groups are distinguished. This indicates that the rarefaction model works better with larger sample sizes. It can be seen in Table 4.31b that the rarefaction model has ordered the eight sites in a similar order of decreasing species richness as the Margalef's index (R_1) but only when data of two seasons are used for both methods

The eight sites have been divided based on altitude so that the first four sites as, S3, S4, S1 and S2 situated at high altitude have higher species richness than the last four being S5, S7, S6, S8 situated at low altitude. Reasons for this pattern of species richness have already been explained in section 4.3 above.

In grassland sites, species richness was increasing with intensity of disturbance (S3, S4, S6, S8). In forest sites, species richness was decreasing with intensity of disturbance. Therefore species richness was influenced by the type and intensity of disturbance, altitude, seasonal variations and vegetation type. Although the order of decreasing species richness across seasons varied among sites, altitude remained a distinguishing factor.

4.5.6 The lognormal distribution model

The lognormal distribution model was used to extract patterns of species assemblages in the eight

sites. It also gives an estimate S^* of total species richness.

Fig. 4.6 (a, b) shows the lognormal model fitted to the data of the study region as a whole and the data as a sum of two sampling seasons (1994/1995) and (1995/1996), for each of the eight sites. The model involves fitting the observed frequency distribution consisting of the number of species found in various abundance classes or octaves to the lognormal distribution (Ludwig and Reynolds, 1988).

It is clear from (Fig.4.6a,b) that all the eight sites show lognormal distribution curves except for S6. This may have been either due to reduced trapping efficiency or actual reduction in insect populations, resulting from heavy rainfall and flooding in the second sampling season at S6. The lognormal curves indicates that these sites have heterogeneous assembly of species with most of the species having intermediate abundances and only a few species represented by very high or very low abundances. It also indicates that these relative abundances are most likely a product of the interplay of many independent factors (Ludwig and Reynolds, 1988).

From (Fig. 4.6b), it can be seen that the order of decreasing number of species, as expected values $S(R)$ and shown in brackets below, which belong to the first octave, that had 1-2 individuals and therefore, the most rare species in each of the eight sites (S1-S8) was:

road verge grassland at high elevation S4 ($S(R)$ =2.45), park S3 ($S(R)$ =2.34), *Acacia*-woodland S5 ($S(R)$ =2.27), macadamia plantation S7 ($S(R)$ =1.59), natural indigenous forest S1 ($S(R)$ =1.41), road verge grassland at low elevation S6 ($S(R)$ =0.82), hay field S8 ($S(R)$ =0.77), pine plantation S2 ($S(R)$ =0.48).

The road verge grassland (S4) with autumn burning had the overall highest number of rare species and pine plantation (S2) in the middle seral stage had the lowest number of rare species.

4.5.6.1 Comparison of lognormal distribution patterns in forests and grasslands at the same altitude

4.5.6.1.1 Lognormal distribution patterns in a natural indigenous forest (S1) and pine plantation (S2) at high altitude

Site 1 had more rare species ($S/R=1.41$) than pine plantation S2 ($S/R=0.48$). But although S2 had few rare species it had many common ones as the last octave is 6 and that at S1 is 5.

4.5.6.1.2 Lognormal distribution patterns in a recreational park grassland (S3) and a road verge grassland (S4) at high altitude

Site 4 had more rare species ($S/R=2.45$) than park S3 ($S/R=2.34$). Both sites seem to have many rare species and many abundant species and few very abundant species.

4.5.6.1.3 Lognormal distribution patterns in Acacia-dominated woodland (S5) and a macadamia plantation (S7) at low altitude

Site 5 had more rare species ($S/R=2.27$) than macadamia plantation S7 ($S/R=1.59$). Site 5 had many rare species and a few very dominant ones, whereas at macadamia plantation S7 the majority of the species are equally dominant.

4.5.6.1.4 Lognormal distribution patterns in a road verge grassland (S6) and a field grassland (S8) at low altitude

Site 6 ($S/R=0.82$) had more rare species than hay field S8 ($S/R=0.77$). But at road verge grassland at low elevation S6, many of the species are equally common and at S8 there are many dominant species.

4.5.6.2 Comparison of the lognormal distribution patterns in primary and secondary forests and grasslands

4.5.6.2.1 Lognormal distribution patterns in primary forests: natural indigenous forest (S1) at high altitude and a natural Acacia-dominated woodland (S5) at low altitude

As primary forests, Acacia-woodland S5 ($S/R=2.27$) had more rare species than natural indigenous forest S1 ($S/R=1.41$). But *Acacia*-woodland S5 had very few dominant species and S1 had many dominant species.

4.5.6.2.2 Lognormal distribution patterns in secondary forests: pine plantation (S2) at high altitude and a macadamia plantation (S7) at low altitude

As secondary forests, macadamia plantation S7 ($S/R=1.59$) had more rare species than pine plantation S2 ($S/R=0.48$) and both sites had many common species.

4.5.6.2.3 Lognormal distribution patterns in primary grasslands: a road verge (S4) at high altitude and a road verge (S6) at low altitude

As primary grasslands, road verge grassland at high elevation S4 ($S/R=2.45$) had more rare species than road verge grassland at low elevation S6 ($S/R=0.82$). S4 also had many common species and a few very abundant species, whereas at S6, the species were almost evenly common.

4.5.6.2.4 Lognormal distribution patterns in secondary grasslands: a recreational park (S3) at high altitude and a field (S8) at low altitude

As secondary grasslands, park S3 had more rare species ($S/R=2.34$) than hay field S8 ($S/R=0.77$). But park S3 had a few very dominant species, whereas S8 had many dominant species.

4.5.6.3 Lognormal model used to estimate theoretical number of species (S^*) available at sites

The total area under the lognormal curve represents the theoretical number of species available for

observation (S^*). This was computed using the equation $S^*=1.77(S_0/a)$ and therefore unobserved number of species can be calculated (Ludwig and Reynolds, 1988). $S(R)$ is the number of species in the R th octave from the mode, S_0 is an estimate of the number of species in the modal octave (the octave with the most species), parameter (a) is an inverse measure of the width of the distribution (i.e., $a = \frac{1}{2}\delta$ where δ is the standard deviation) and 1.77 is a constant (product of the mathematical properties of the lognormal distribution). Table 4.32 gives a summary of values calculated from fitting the lognormal model for each of the eight sites and for the whole study area. According to this model, the theoretical number of species (S^*) per site in decreasing order was: S7($n=23$) macadamia plantation, S4($n=22$) road verge grassland, S1($n=17$) indigenous forest, S5($n=15$) *Acacia* woodland, S2($n=14$) pine plantation, S3($n=13$) park, hay field S8($n=7$) field of hay. The model was not able to be applied to the data at road verge grassland at low elevation S6 may be due to reduced trapping efficiency or actual reduction in insect populations, resulting from heavy rainfall and flooding in the second sampling season at S6.

4.5.7 Comparison of three species richness indices: Margalef's index (R_1), rarefaction model and the theoretical number of species (S^*)

Table 4.31 b shows order of decreasing species richness of the eight sites using the rarefaction model and Margalef's index (R_1). The theoretical number of species (S^*) from the lognormal model is shown in Table 4.32. This is discussed in detail in section 5.4.3.

The Margalef's index (R_1) gave similar patterns as the rarefaction model using data as a sum of two seasons, and the eight sites were ordered in such a manner that, the first four sites were situated at high altitude and had higher species richness and the last four were at low altitude and had lower species richness. When data from individual annual seasons was used, the Margalef's index (R_1) and the rarefaction model gave dissimilar patterns to those produced using two seasons' data. Therefore, it appears that these two models give more consistent results when two seasons' data are used.

According to the rarefaction model and Margalef's index (R_1) models, the number of species per site in decreasing order was: park (S3); road verge (S4); mist belt indigenous forest (S1); pine plantation (S2); savanna woodland (S5); macadamia plantation (S7); road verge grassland at low altitude (S6); field of hay (S8). In forest landscapes, the natural indigenous mistbelt forest (S1) was the most rich in species and the macadamia plantation (S7) with intensive irrigation was the least poor in carabid species. In grassland landscapes, the park was the most rich in species and S8 field of hay was the least poor.

According to the lognormal theoretical number of species model (S^*), the number of species per site in decreasing order was: macadamia plantation (S7); road verge (S4); mist belt indigenous natural forest (S1); savanna woodland (S5); pine plantation (S2); park (S3); field of hay (S8). In forest landscapes, macadamia plantation (S7) with intensive irrigation was the most rich in carabid species followed by the natural indigenous mistbelt forest (S1) and the pine plantation (S2) in the middle successional stage was the least species rich. In grassland landscapes, S4 a road verge grassland with prescribed alternating annual autumn burning disturbance, was the most rich in carabid species and a field of hay mown once in a year had the least number of species.

4.5.8 Caswell's neutral model used to estimate environmental stress levels

Increasing levels of environmental stress have generally been considered to decrease diversity (H'), i.e. decrease species richness (Margalef's R_1) and decrease evenness (J') which increases dominance (Connell, 1978; Huston, 1979).

The evenness component of diversity can be compared with some theoretical expectation of diversity, given the number of individuals and species present. Observed diversity has been compared with predictions from Caswell's neutral model (Caswell, 1976). This model constructs an ecologically 'neutral' community with the same number of species and individuals as the observed community, assuming certain community assembly rules (random births/deaths and random immigration/emigrations) and no interactions between species. The deviation statistic V is then

Sites	Sampling seasons	No. species	Sampling replicate month at asymptote point on curve	Increase of species caught over summer Sept-March	Additional species caught over autumn/winter April-June	Comparison of numbers caught over seasons
1	94/95	7	10 - March	2 - 7	0	94/95 < 95/96
	95/96	8	11 - April	4 - 7	1 (130a)	
2	94/95	7	10 - March	3 - 7	0	94/95 > 95/96
	95/96	7	11 - April	2 - 6	1 (115b)	
3	94/95	5	10 - March	1 - 5	0	94/95 < 95/96
	95/96	7	11 - April	2 - 4	3 (115b,35a,147)	
4	94/95	12	9 - Feb	3 - 12	0	94/95 > 95/96
	95/96	9	10 - March	1 - 8	0	
5	94/95	6	12 - May	0 - 4	2 (35a,147)	94/95 < 95/96
	95/96	8	9 - Feb	2 - 8	0	
6	94/95	6	11 - April	1 - 5	1 (126)	94/95 > 95/96
	95/96	3	9 - Feb	2 - 3	0	
7	94/95	12	11 - April	7 - 11	1 (147)	94/95 >> 95/96
	95/96	6	11 - April	2 - 4	2 (133,276)	
8	94/95	4	9 - Feb	1 - 4	0	94/95 = 95/96
	95/96	3	4 - Sept	3 - 3	0	
Yearly totals	94/95	29	10 - March	13-29	0	94/95 > 95/96
	95/96	26	11 - March	9-26	4	
Whole period	94-96	35	11 - April	-	1	-

Table 4.29: Summary of information on cumulative number of species obtained from Table 4.2-4.20 and Fig. 4.1 (a) (b) (c), for the whole study period. The first sampling season is June 1994-May 1995. The second sampling season is June 1995-May 1996. Column six lists the number of additional new species caught over autumn/winter. Numbers in brackets are species code numbers, see Table 4.1 for actual names of species.

Site	1994/1995 V	1995/1996 V	Sum V
1	+ 0.29	+ 0.91	+ 0.58
2	+ 1.40	+ 0.40	+ 1.11
3	+ 0.56	- 0.31	+ 0.44
4	+ 0.67	+ 0.52	+ 0.65
5	- 0.84	- 1.48	- 2.14
6	+ 0.96	+ 0.03	+ 0.04
7	- 0.55	+ 0.81	- 0.41
8	- 1.77	+ 1.46	+ 0.22

Table 4.30: V statistic that compares observed diversity (H') with that predicted from Caswell's neutral model for each of the eight sites. The V statistic was calculated using data over the first sampling season (June 1994-May 1995), the second sampling season (June 1995-May 1996) and sum of the two seasons (June 1994-May 1996).

Sample size (n)	Expected number of species E (Sn) per site (S1-S8)																							
	1st season, June 1994-May 1995								2nd season, June 1995-May 1996								Sum of two seasons, (June 1994-May 1996)							
	S1	S2	S3	S4	S5	S6	S7	S8	S1	S2	S3	S4	S5	S6	S7	S8	S1	S2	S3	S4	S5	S6	S7	S8
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	3	3	3	4	2	3	3	2	3	3	3	3	2	2	3	2	3	3	3	3	2	2	3	2
10	4	4		5	3	4	3	2	5	4	4	4	3	2	3	3	5	4	5	5	3	3	3	3
15	5	5		6	3	4	4	3	6	4	5	5	3	2	3	3	6	5	7	6	3	3	4	3
20	5	5		7	3	4	4	3	6	4		6	4	2	4	3	6	5	7	7	4	3	4	3
25	6	5		8	4	5	4	3	7	5		6	4	3	4	3	7	5	8	8	4	4	4	4
30	6	6		9	4	5	5	3	7	5		6	5	3	4	3	7	5	9	8	4	4	4	4
35		6		9	4	5	5	3	8	5		7	5	3	4	3	8	6	9	9	5	4	5	4
40		6		9	4	5	5	3		5		7	5		4	3	8	6		9	5	4	5	4
45		6		10		5	5			6		7			4	3	8	6		9	5	4	5	4
50		6		10		5	5			6		7			4		9	6		9	6	4	5	4

Table 4.31(a): Rarefaction model for comparison of species richness between the eight sites (S1-S8), over the first season, second season and sum of the two seasons based on a standard sample size of n=5, n=15 and n=35 respectively.

	Order of decreasing species richness across the eight sites (1-8).		
	94/95	95/96	Sum (94-96)
Rarefraction model n = 5	4: 1 2 3 6 7: 5 8	1 2 3 4 7: 5 6 8	1 2 3 4 7: 5 6 8
n = 15	-	1: 3 4: 2: 5 7 8: 6	3: 14: 2: 7: 5 6 8
n = 35	-	-	3 4: 1: 2: 5 7: 6 8
Margalef Index R1	4 7 1 3 2 6 5 8	1 3 4 5 2 7 8 6	3 4 1 2 5 7 6 8
Theoretical No. of Species S*	-	-	7 4 1 5 2 3 8 6

Table 4.31(b): Comparison of three species richness indices namely rarefraction model obtained from Table 4.31(a), Margalef's Index (R1) obtained from Table 4.27 and the theoretical number of species (S*) from the lognormal model (Table 4.32).

	Sites							Whole Study Area
	1	2	3	4	5	7	8	
Theoretical No. of Species S*	17	14	13	22	15	23	7	39
Observed Species	10	8	10	14	11	13	5	35
Unobserved Species	7	6	3	8	4	10	2	4

Table 4.32: Summary of values calculated from fitting the lognormal to the species data for each of the eight sites (1-8), and to the species data for the whole study area. At Site 6, $a = 0$, therefore, it is not possible to calculate S*.

determined which compares the observed diversity (H') with that predicted from the neutral model ($E(H')$). A value of zero for the V statistic indicates neutrality, positive values indicate greater diversity than predicted and negative values lower diversity. Values greater than +2 or less than -2 indicate significant departures from neutrality (Caswell, 1976). The computer program CASWELL in PRIMER (Clarke and Warwick, 1994) was used to compute the V statistic for the eight sites (Table 4.30). The diversity using data of two seasons in the *Acacia*-dominated woodland (S5) was significantly below neutral model predictions (-2.14), and the diversity at all other sites was close to neutrality. According to this model, the carabid community was under some environmental stress in the *Acacia*-woodland (S5). Indeed this site had the lowest evenness value (Fig. 4.5).

4.6 GRAPHICAL/DISTRIBUTIONAL MODELS FOR DETECTING EFFECTS OF ENVIRONMENTAL STRESS

The purpose of graphical/distributional representations is to extract information on patterns of relative species abundances without reducing that information to a single summary statistic such as a diversity index. Unlike multivariate methods, these distributions may extract universal features of community structure which are not a function of the specific taxa present, and may therefore be related to levels of biological stress (Clarke and Warwick, 1994). Two plots of this type are geometric abundance plots and ranked species abundance (dominance) curves.

4.6.1 x2 geometric plots

Gray and Pearson (1982) recommended plotting the number of species in x2 geometric abundance classes as a means of detecting the effects of environmental stress. These are plots of the number of species represented by only one individual in the sample (class 1), 2-3 individuals (class 2), 4-7 (class 3), 8-15 (class 4) etc.

In unpolluted situations there are many rare species and the curve is smooth with its mode well to the left. In polluted situations there are fewer rare species and more abundant species so that higher

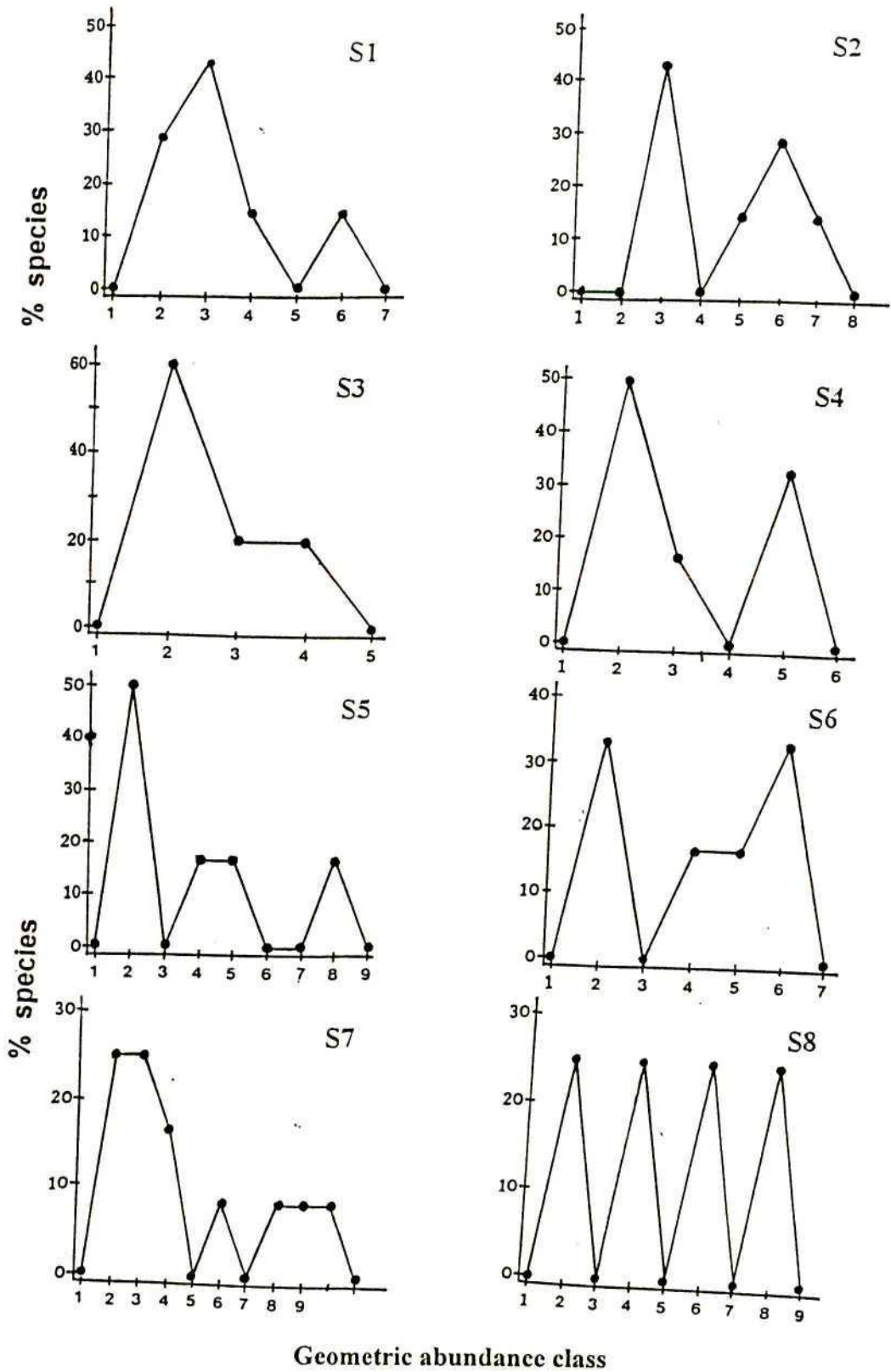


Figure 4.7(a): Plots of $\times 2$ geometric species abundance classes, using data over the first sampling season (June 1994-May 1995), shown for each of the eight sites (S1-S8).

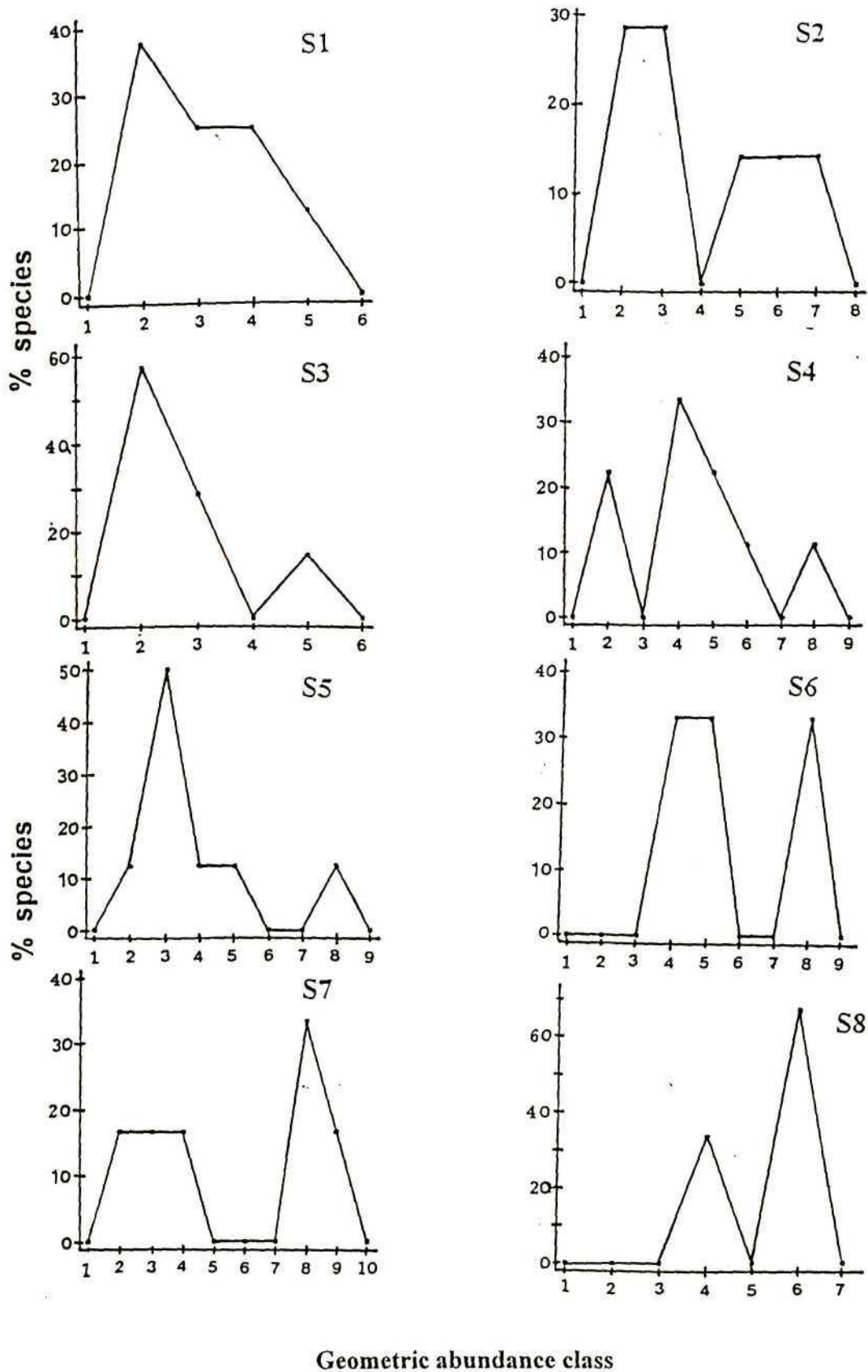


Figure 4.7(b): Plots of $\times 2$ geometric species abundance classes, using data over the second sampling season (June 1994-May 1996), shown for each of the eight sites (S1-S8).

geometric abundance classes are more strongly represented. Gray and Pearson (1982) further suggest that it is the species in the intermediate abundance classes 3 to 5 that are the most sensitive to pollution induced changes and might best illustrate the differences between polluted and unpolluted sites (i.e. this is a way of selecting 'indicator' species objectively).

Fig. 4.7(a,b) shows plots of x^2 geometric species abundance classes over the first sampling season (1994/1995) and second sampling season (1995/1996) respectively.

4.6.1.1 Comparison of x^2 geometric plots in the eight sites

4.6.1.1.1 x^2 geometric plots in natural indigenous forest (S1) and pine plantation (S2) at high altitude

Data of two sampling seasons plots (1994-1996) showed that the indigenous natural forest had a higher percentage (30%) of class 2 individuals of rare species than the pine plantation with 13% rare species. The percentage of class 2 individuals varied across seasons. The structural patterns in each site was maintained across the seasons (Fig. 4.7 a, b).

4.6.1.1.2 x^2 geometric plots in a recreational park (S3) and a road verge (S4) at high altitude

Data of two sampling seasons plots (1994-1996) showed that, the park lawn had a higher percentage (40%) of class 2 individuals of rare species than a road verge with autumn burning with (22%) rare species. The overall structural pattern across seasons at S3 was similar. However, at S4, the percentage of rare species during the first sampling season after the site burnt, was higher (50%) than the second sampling season with no burning (22%). In addition, there was a drop in class 3 to 5 individuals over the first season with burning disturbance.

4.6.1.1.3 x^2 geometric plots in Acacia-dominated woodland (S5) and macadamia plantation (S7) at low altitude

Data of two sampling seasons plots (1994-1996) showed that *Acacia*-dominated natural forest had a higher percentage (37%) of class 2 individuals of rare species than macadamia plantation under

intensive agricultural management, with (31%) rare species. The percentage of class 2 individuals varied across seasons such that in the second season, macadamia plantation S7 (17%) had a higher percentage of rare species than *Acacia*-woodland S5 (12%). The structural patterns across the two seasons at S5 were similar, (Fig. 4.7a, b). However at macadamia plantation S7, class 5-7 individuals were absent in the second season, may be due to the heavy rainfall and flooding that occurred in this region. Although S5 was adjacent to macadamia plantation S7, the reason why macadamia plantation S7 was affected more by heavy rains may be the presence of a closed tree canopy and thick litter layer for shelter.

4.6.1.1.4 x2 geometric plots in a road verge grassland (S6) and a field grassland (S8) at low altitude

Data of two sampling seasons plots (1994-1996) showed that, a road verge (S6) which was burnt during the first sampling season had a higher percentage (34%) of class 2 individuals of rare species than S8 a field with (20%). During the first sampling season, road verge grassland at low elevation S6 had class 2 individuals present and a drop in class 3 to 5 individuals was observed due to burning disturbance at this site. In the second season, at S6, class 2 individuals were absent and the burning intensity at this site was low and class 3 to 5 individuals were not affected. The absence of rare species as class 2 individuals both at S6 and hay field S8 in the second season, may be a result of heavy rains with heavy flooding which took place in this region (see Fig. 4.7a,b).

4.6.1.3 Comparison of x2 geometric plots in primary and secondary forests and grasslands

4.6.1.3.1 x2 geometric plots in primary forests: natural indigenous forest (S1) and natural Acacia-dominated woodland (S5)

Data as sum of two sampling seasons (1994-1996) showed that *Acacia*-dominated natural forest at low altitude had a higher percentage (37%) of class 2 individuals of rare species than an indigenous natural forest at high altitude with 30% rare species. The percentage of class 2 individuals varied across seasons within each site. The structural pattern across the two seasons per site remained similar (Fig. 4.7a,b).

4.6.1.3.2 x2 geometric plots in secondary forests: pine plantation (S2) and macadamia plantation (S7)

Data of two sampling seasons plots (1994-1996) showed that, a macadamia plantation at low altitude had a higher percentage (31%) of class 2 individuals of rare species than the pine plantation at high altitude with (13%) rare species. The percentage of class 2 individuals varied across seasons within each site. The structural pattern across the two seasons per site remained similar (Fig.4.7a,b).

4.6.1.3.3 x2 geometric plots in primary grasslands: a road verge (S4) at high altitude and a road verge (S6) at low altitude

Data of two sampling seasons plots (1994-1996) showed that, grassland in a road verge at low altitude had a higher percentage (34%) of class 2 individuals of rare species than a grassland in a road verge at high altitude with (22%) rare species. The structural pattern across each landscape changed from one season to the next due to the burning disturbances at these sites.

4.6.1.3.4 x2 geometric plots in secondary grasslands: recreational park (S3) and a field of hay (S8)

Data of two sampling seasons plots (1994-1996) showed that a park lawn had a higher percentage (40%) of class 2 individuals of rare species than a grassland field with 20% rare species. The percentage of class 2 individuals varied across seasons but the pattern was maintained within each landscape except at S8, which showed absence of class 2 individuals in the second season (Fig. 4.7a,b).

4.6.2 Rank abundance (dominance) curves

Fig. 4.8 shows species rank abundance curves from two sampling seasons (1994-1996). Rank abundance curves over the first sampling season (1994/1995) and second sampling season (1995/1996) gave similar patterns. These plots are based on the ranking of species in decreasing order of their importance in terms of abundance from most common to most rare. The distribution of communities at each site showed lognormal curves, indicating that they are species rich communities. This is also supported by the actual fitting of the data to the lognormal model (section

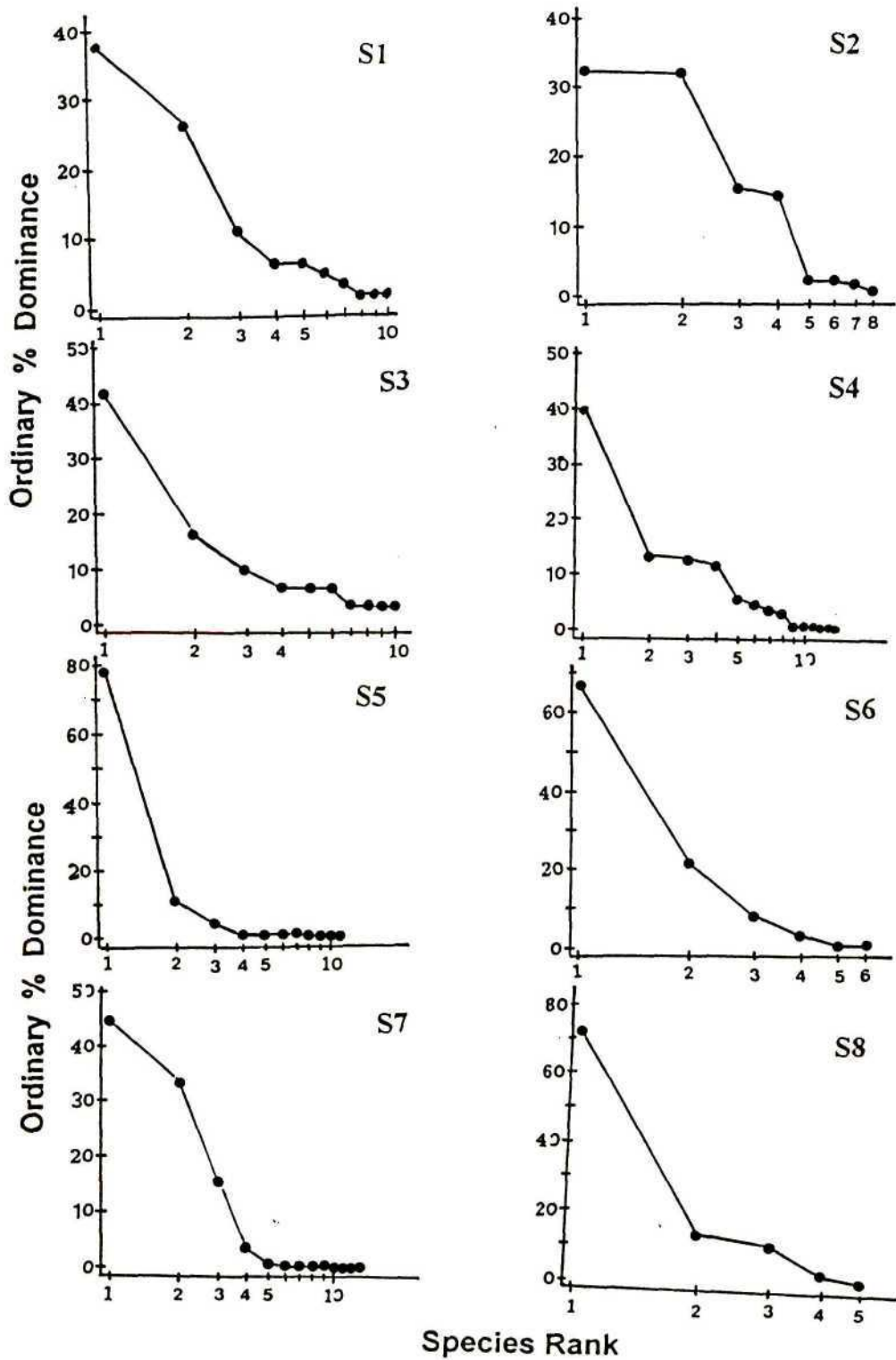


Figure 4.8: Plots of ranked species abundance (dominance) curves, using data as the sum of two sampling seasons (June 1994-May 1996). Species are ranked in decreasing order of their importance in terms of abundance from most common to most rare, and shown for each of the eight sites (S1-S8).

4.5.6 and Fig. 4.6a,b). However, because *Acacia*-woodland differs from all the other sites by being dominated by one species, the rank abundance curves (Fig. 4.8) were subjected to further treatment by changing the abundance values on the x axis to logs ($\ln x$). This was considered and carried out but did not make a change in the patterns.

4.7 MULTIVARIATE ANALYSIS OF SPECIES DATA

4.7.1 Community classification and ordination using PRIMER

The PRIMER programs CLUSTER and MDS, were used to carry out classification and ordination of samples through hierarchical clustering and non-metric multidimensional scaling (MDS).

4.7.1.1 Classification and MDS ordination at the landscape level

Fig. 4.9 shows the classification of the eight sites through a dendrogram for hierarchical clustering using group average linking of Bray-Curtis similarities calculated on 4th root-transformed abundance data as a sum of two sampling seasons. Classification results of data over the first sampling season and second sampling seasons showed similar patterns.

It can be seen in Fig. 4.9 that, at around 50% similarity level, six groups can be determined as S1&2: S3: S4: S7: S5: S6&8. The similarity between groups S1&2 was 63.38% and S6&8 was 64.85%. These groupings, when superimposed on the respective MDS ordinations (Fig. 4.10a, b, c), it became clear that the agreement between the two techniques was excellent. The stress for (Fig. 4.10 a, b, c) was low (0.13, 0.09, 0.15 respectively), giving confidence that the 2-dimensional MDS plots are a good representation of the landscape relationships (Clarke and Warwick, 1994).

Species analysis was carried out using the PRIMER program SIMPER to determine good discriminator species, i.e. species responsible for the creation of the six groups produced by cluster analysis (Fig. 4.9) and MDS analysis (Fig. 4.10). The discriminator species are listed in Table 4.33.

The MDS ordinations of data of individual sampling seasons and as sum of the two seasons (Fig. 4.10) indicate a clear separation of sites along geographical location (altitude) where (S1, S2, S3,

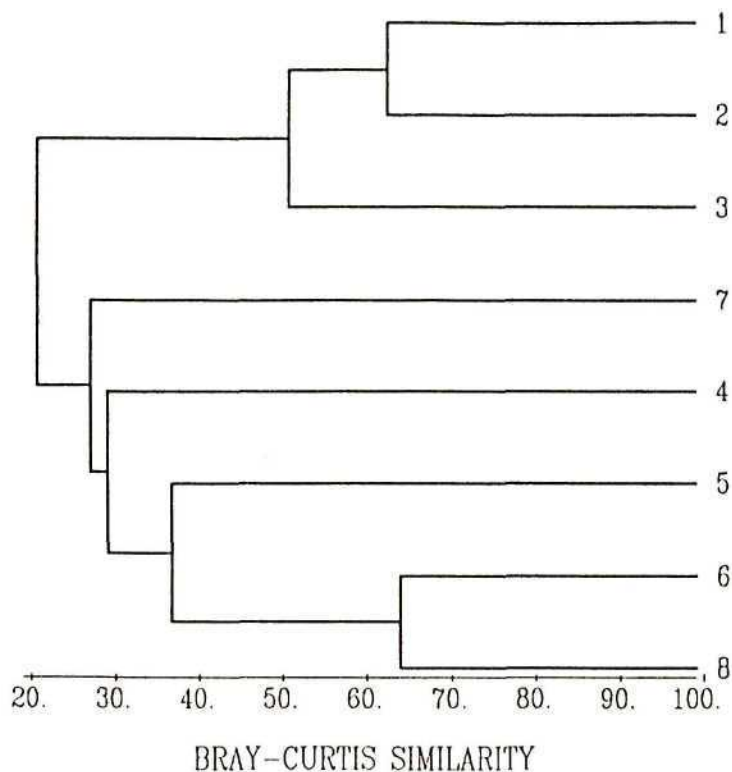


Figure 4.9: Dendrogram for hierarchical clustering of the eight sites (1-8), using group-average linking of Bray-Curtis similarities calculated on 4th root-transformed abundance data of carabids and cicindelids as sum of two seasons (June 1994-May 1996), using PRIMER.

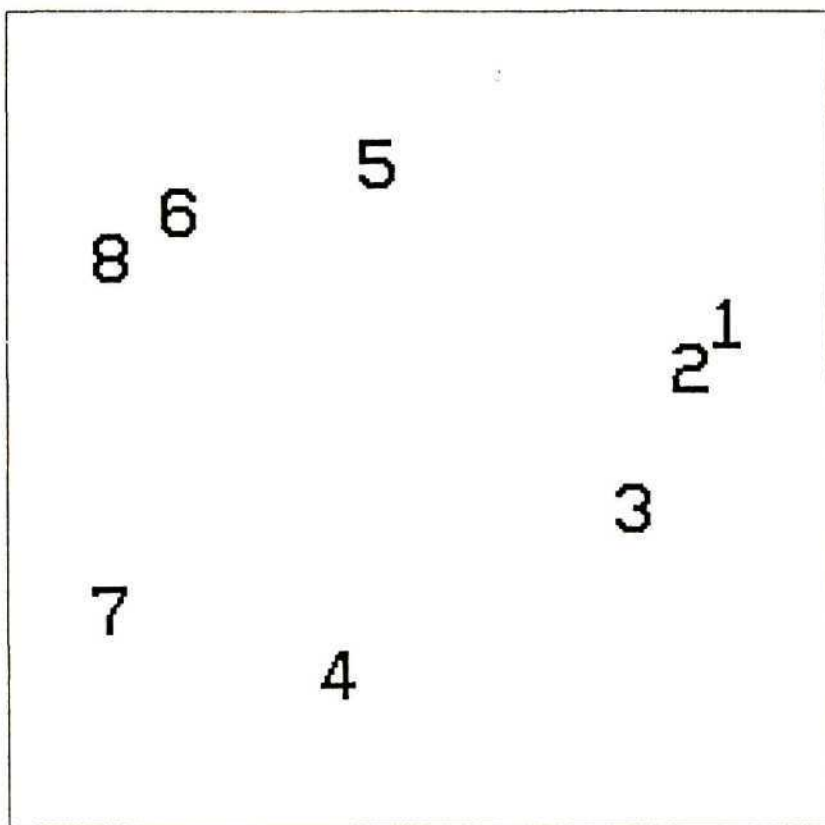


Figure 4.10(a): MDS ordination of the eight sites (1-8) based on 4th root-transformed abundance data and Bray-Curtis similarities of carabid and cicindelid abundance data as sum of two sampling seasons (June 1994-May 1996), using PRIMER. Stress=0.13.

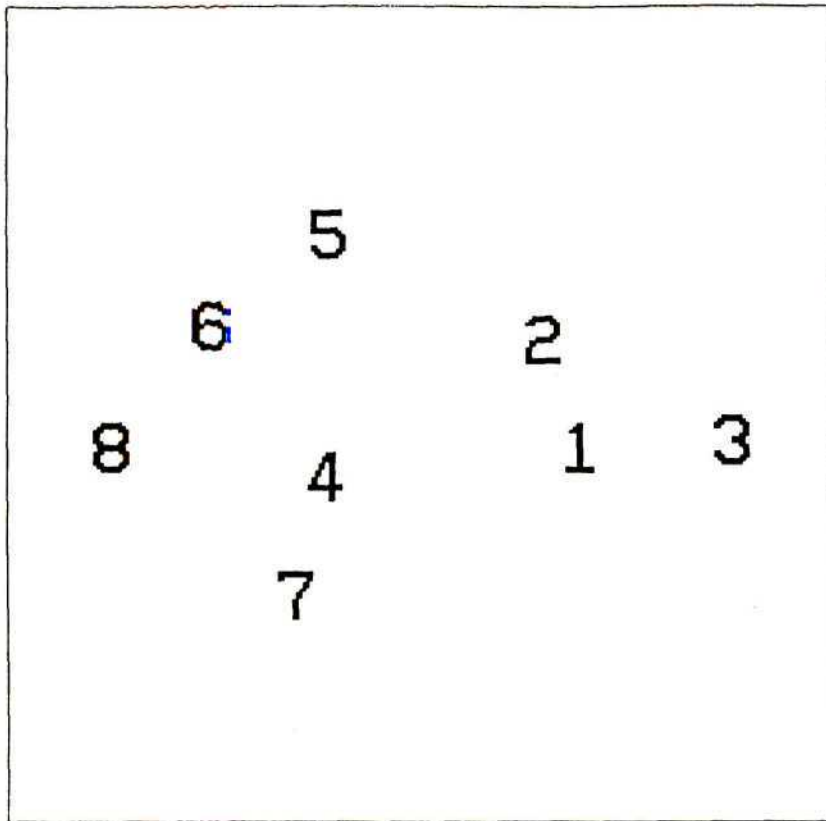


Figure 4.10(b): MDS ordination of the eight sites (1-8) based on 4th root-transformed abundance data and Bray-Curtis similarities of carabid and cicindelid abundance data over the first sampling season (June 1994-May 1995), using PRIMER. (Stress=0.09).

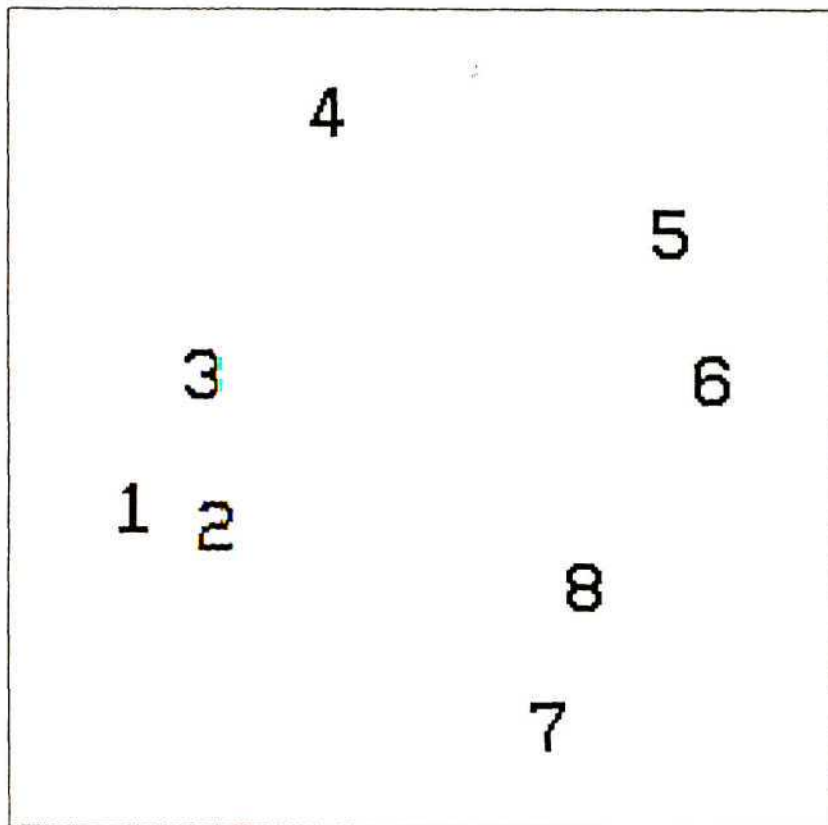


Figure 4.10(c): MDS ordination of the eight sites (1-8) based on 4th root-transformed abundance data and Bray-Curtis similarities of carabid and cicindelid abundance data over the second sampling season (June 1995-May 1996), using PRIMER. (Stress=0.15).

S4), situated in the higher altitudes of the Escarpment Zone are on one side of the diagram and (S5, S6, S7, S8) are in the lower altitudes of the Savanna Zone, are on the opposite side of the diagram.

The MDS ordination of data over the first sampling season (Fig. 4.10b), placed S4 (a road verge grassland at high altitude) closer to S6 (a road verge grassland at lower altitude), meaning that they were more similar. Whereas, in the second season, these two sites were clearly separated along an altitude gradient (Fig. 4.10c). The intensity of autumn burning at these two sites had an effect on the distribution of the beetles, which influenced this mapping. For example, the cicindelid species *D. gilvipes* was recorded at both sites during the first season after intensive burning. In the second sampling season, the intensity of burning at S6 was lower and this species was never recorded or observed. At S4, this species was recorded and observed in the region where the grassland had been cut and none was seen or observed in the region of tall grasses.

4.7.1.1.1 Comparisons of forests and grasslands at high altitude using MDS ordination

In forest sites at high altitude, S1 (a natural indigenous forest) and S2 (a pine plantation), were grouped close together with a similarity of 63.38%. These two forests shared many species except three species that were only recorded at S1 in low abundance and not S2 being *Lebia insidiosa* (130a), *Hystrichopus atratus* (147), *Systolocranius alternaris* (254). The Harpalini sp. (35a) was recorded at S2 and not S1. The most common species between the two sites were *Cophosomorpha pseudocastellani* (38), *Abacetus* sp. (213), and *Lebiini* sp. (32) which reached maximum abundance at S2. The most common species at S1 was *Metagonum gilvipes* (115a), but it was recorded in low abundance at S2.

In grassland sites at high altitude, S3 (a park) was more similar to S1&2, with a similarity of 51.82% than it was to S4 (a grassland road verge) which was similar to S3 by 29.28% as they had very few species in common. The actual discriminating species can be seen in Table 4.33.

The MDS ordination patterns of all sites was maintained for data across the two seasons (except for S4 and S6) and the sum of the two seasons, Fig. 4.10.

4.7.1.1.2 Comparisons of forests and grasslands at low altitude using MDS ordination

The macadamia plantation (S7) and the *Acacia*-dominated forest (S5) are distinctly separated and very far apart (only 23.6% similar).

The grassland habitat at S6 and S8 are grouped close together and are 64.85% similar. The species recorded at S6 and not S8 were *Callistomimus caffer* (178) and *Dromica gilvipes* (250a). The species recorded at S8 and not S6 was *Hyparpalus tomentosus* (133). The species mentioned above constitute the discriminating species at these grassland sites (S6&8). The same pattern was maintained across the two sampling seasons (Fig. 4.10).

4.7.1.2 Classification and MDS ordination at the point habitat level

Fig. 4.11 shows dendrograms for hierarchical clustering of the 32 point habitats over the eight sites and the MDS ordinations are shown in (Fig. 4.12a,b,c) using abundance data as sum of two seasons, first sampling season and second sampling season.

The MDS ordination of data as sum of two seasons (Fig. 4.12a) was able to distinguish the eight sites. The carabid and cicindelid community is seen to change from site to site but also appears to differ from point habitat to point habitat per site.

Data in the first sampling season grouped the hierarchical clustering of point habitats within each landscape closer together (Fig. 4.11b) but the respective MDS ordination did not match this clustering and was unable to separate the various site groups (Fig. 4.12b).

Data in the second sampling season did not group clearly the point habitat numbers 1, 2, 3, 4 belonging to Site 1 and point habitat numbers 9, 10, 11, 12 belonging to Site 3, (Fig. 4.12c). At Site 4, it can be seen that point habitat number 13 was grouped far away from point habitats 14, 15 and 16, which were grouped closer together. This shows that point habitat number 13 was very dissimilar to the rest. This can be related to the fact that, during this period, grass was cut along a narrow strip of five metres under the electricity posts as a maintenance routine which had the effect of increasing the carabid and cicindelid abundance at these point habitats relative to the point habitat numbers 14, 15 and 16 with tall grass.

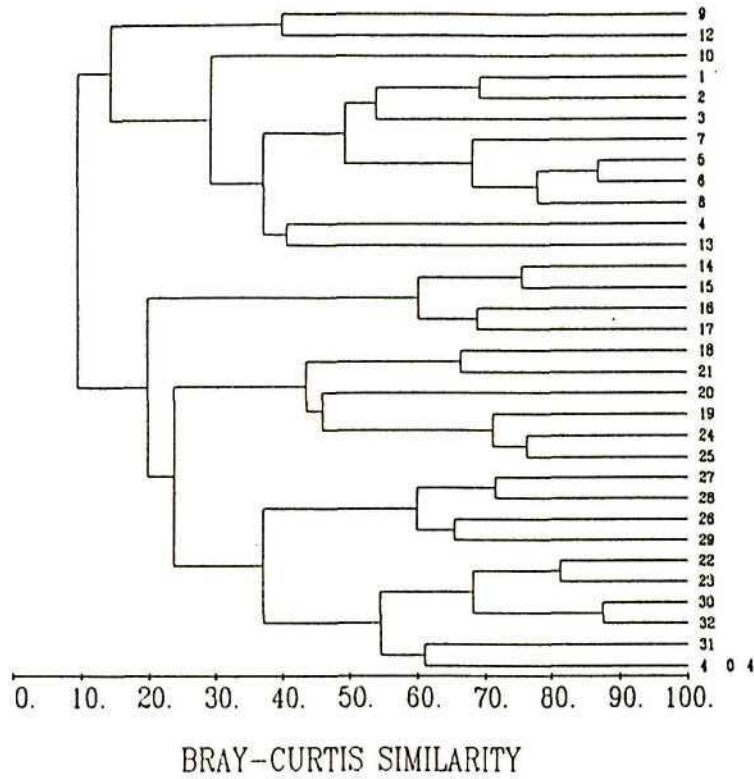


Figure 4.11: Dendrogram for hierarchical clustering of the 32 point habitats (1-32) in the eight sites, using group-average linking of Bray-Curtis similarities calculated on 4th root-transformed abundance data of carabids and cicindelids as sum of two seasons (June 1994-May 1996), using PRIMER.

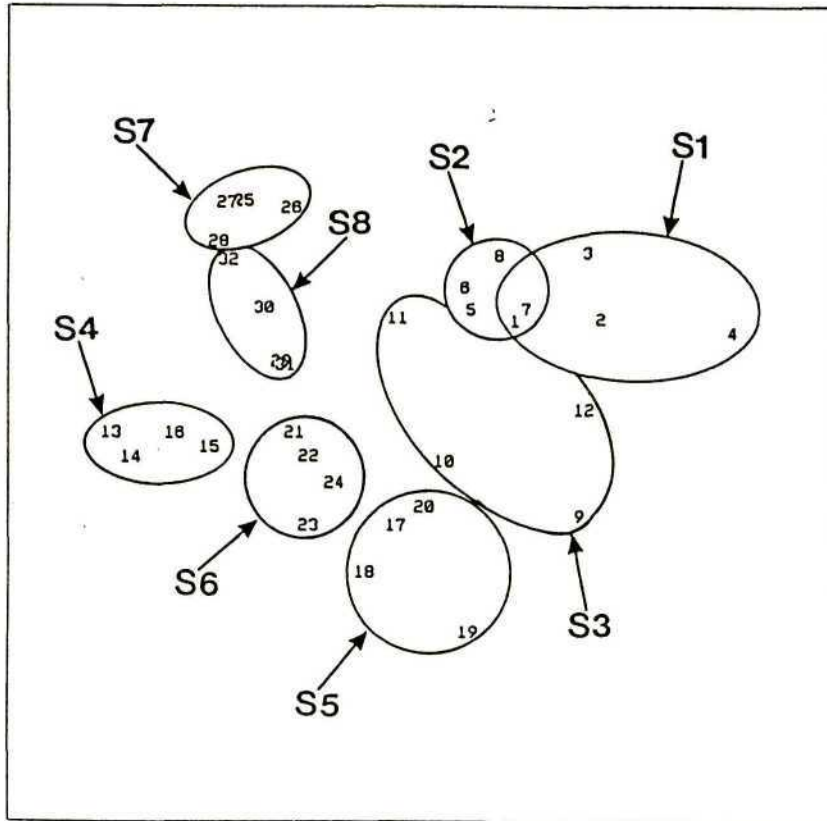


Figure 4.12(a): MDS ordination of the 32 point habitats (1-32) in the eight sites (S1-S8) based on 4th root-transformed abundance data and Bray-Curtis similarities of carabid and cicindelid abundance data as sum of the two sampling seasons (June 1994-May 1996), using PRIMER. (Stress=0.19).

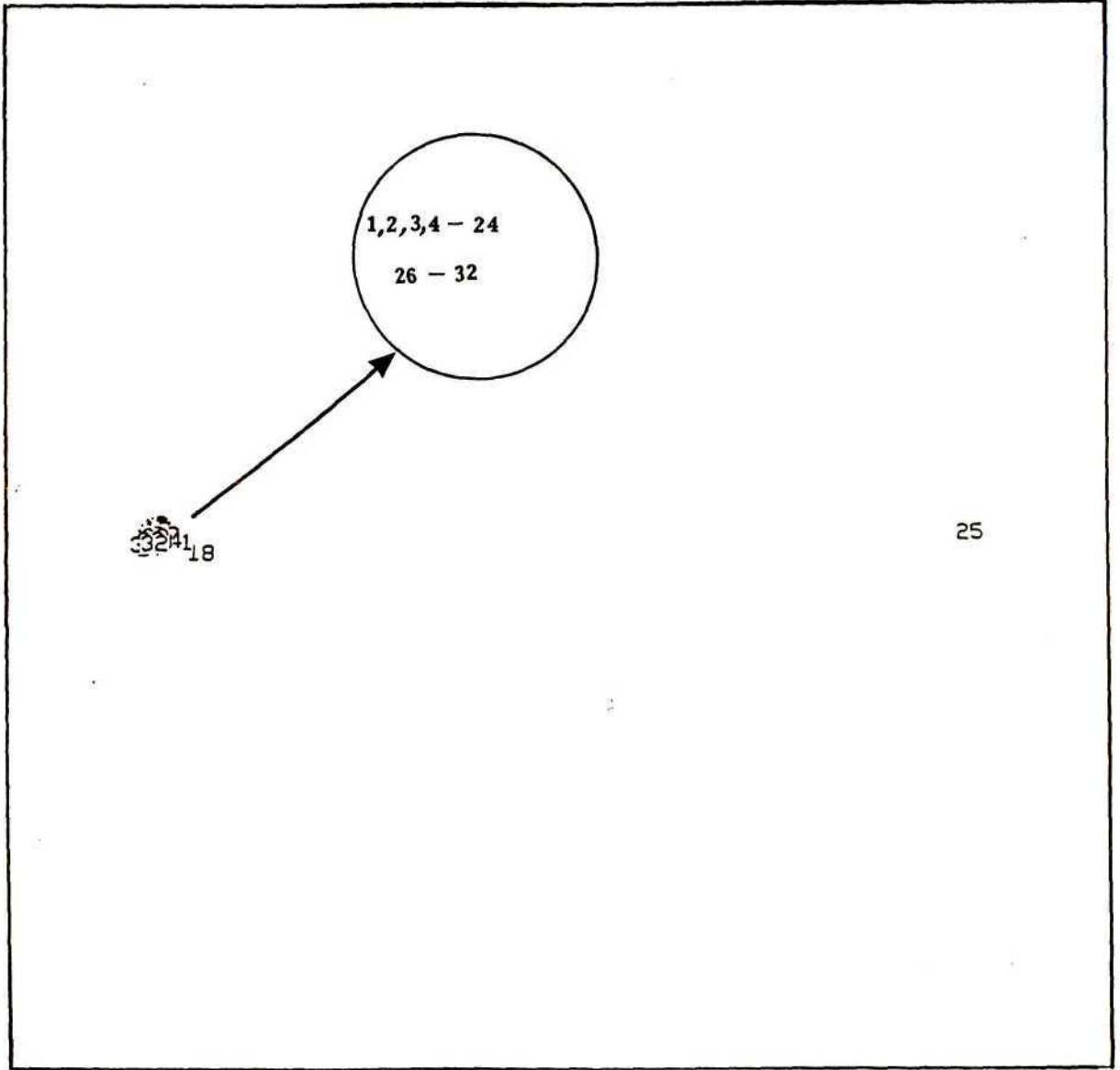


Figure 4.12(b): MDS ordination of the 32 point habitats (1-32) over the eight sites based on 4th root-transformed abundance data and Bray-Curtis similarities of carabid and cicindelid abundance data over the first sampling season (June 1994-May 1995), using PRIMER. (Stress=0.01).

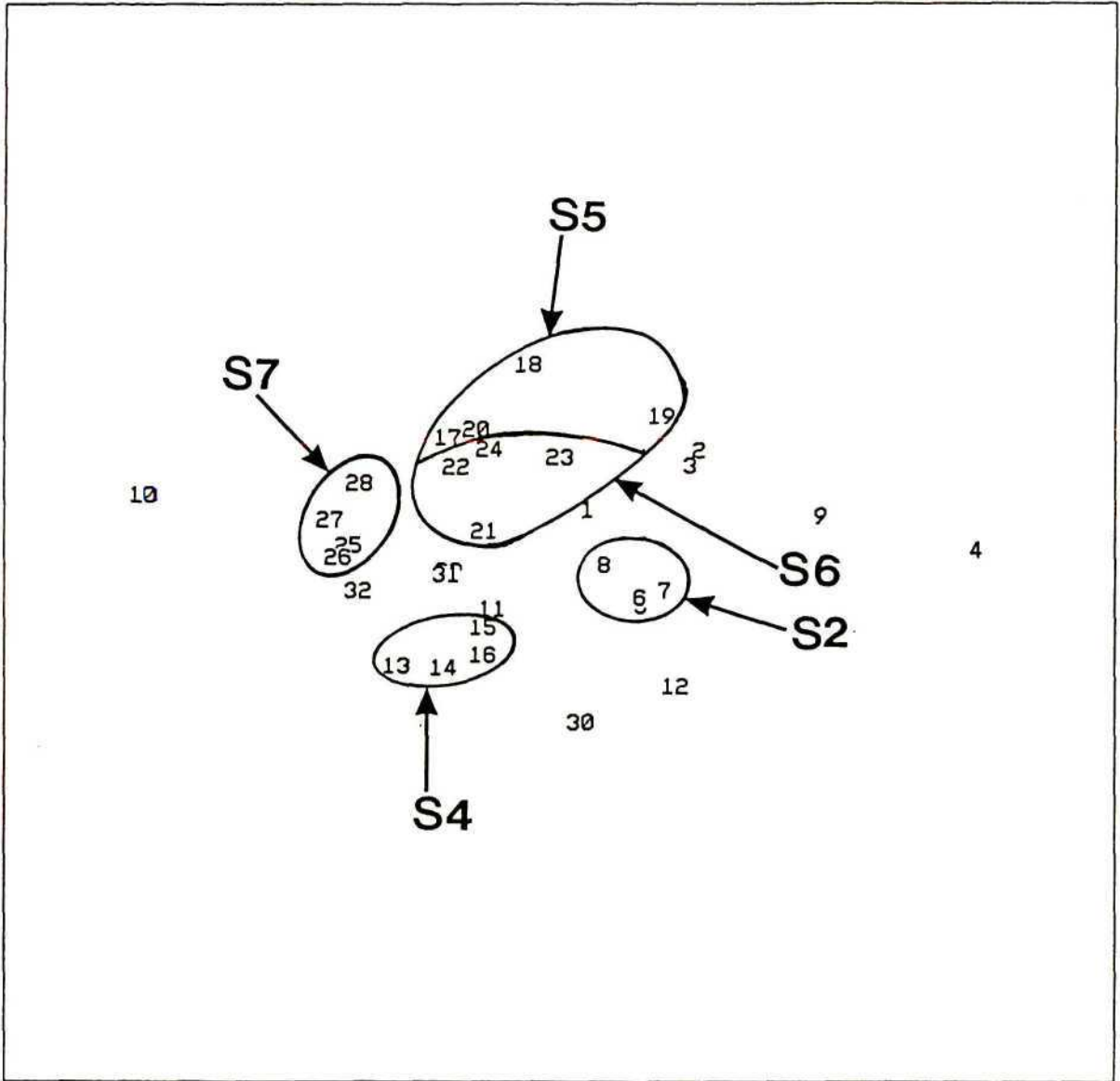


Figure 4.12(c): MDS ordination of the 32 point habitats (1-32) over the eight sites (S1-S8) based on 4th root-transformed abundance data and Bray-Curtis similarities of carabid and cicindelid abundance data over the second sampling season (June 1995-May 1996), using PRIMER. (Stress=0.15).

4.7.1.3 Linking community structure to environmental variables

4.7.1.3.1 PCA analysis of environmental data

Fig. 4.13 displays the first two axes of a PCA ordination of all the environmental variables listed in section 3.3.4. The first component was a moisture/sand gradient which accounted for 30% of the variability and the second component was a geographical or altitude gradient of Savanna and Escarpment, which accounted for 27% of the variability. These two components accounted for 57% of the variability.

When Fig. 4.13 was compared with (Fig. 4.10a), of an MDS ordination based on biota (species data), the eight sites were grouped in similar patterns, and were separated based on altitude. Those situated in the Escarpment Zone (S1, S2, S3, S4) are on one side of the diagram, while those in the lower altitude of the Savanna Zone (S5, S6, S7, S8) are on the opposite side of the diagram, indicating that the 17 variables measured can explain the species patterns observed.

4.7.1.3.2 Linking community structure to univariate environmental variables

Having described carabid and cicindelid species data by multivariate MDS ordination, (Fig. 4.10a), the relation of this pattern to individual environmental variables measured in Table 3.2 was best visualized by representing the values of these eight variables as symbols of increasing size and superimposing these symbols on the biotic MDS ordination (Fig. 4.14a-I), which revealed a more informative picture of the gradients of individual environmental variables across the eight sites.

Fig. 4.14b, confirmed results of the PCA analysis of environmental variables, which showed that, the main axis of biotic MDS was one of increasing moisture/sand in the A1 horizon along a geographical location or altitude gradient. Sites (S1, S2, S3, S4) situated at high altitude with a cooler climate were made of more sandy soils than those (S5, S6, S7, S8) situated at low altitude with a savannah climate. Moisture was correlated with sand and was lowest where sand was highest (Fig. 4.14c). The grassland road verge (S4) had the highest amount of sand in the A1 horizon and the least soil moisture. All the four cicindelids recorded in this study were found at this site. These were *Cicindela marginella inanis*, *Dromica tuberculata carinulata*, *Dromica gilvipes* and the undescribed Cicindelini sp. (250b). The cicindelid *D. gilvipes* was recorded at a similar grassland

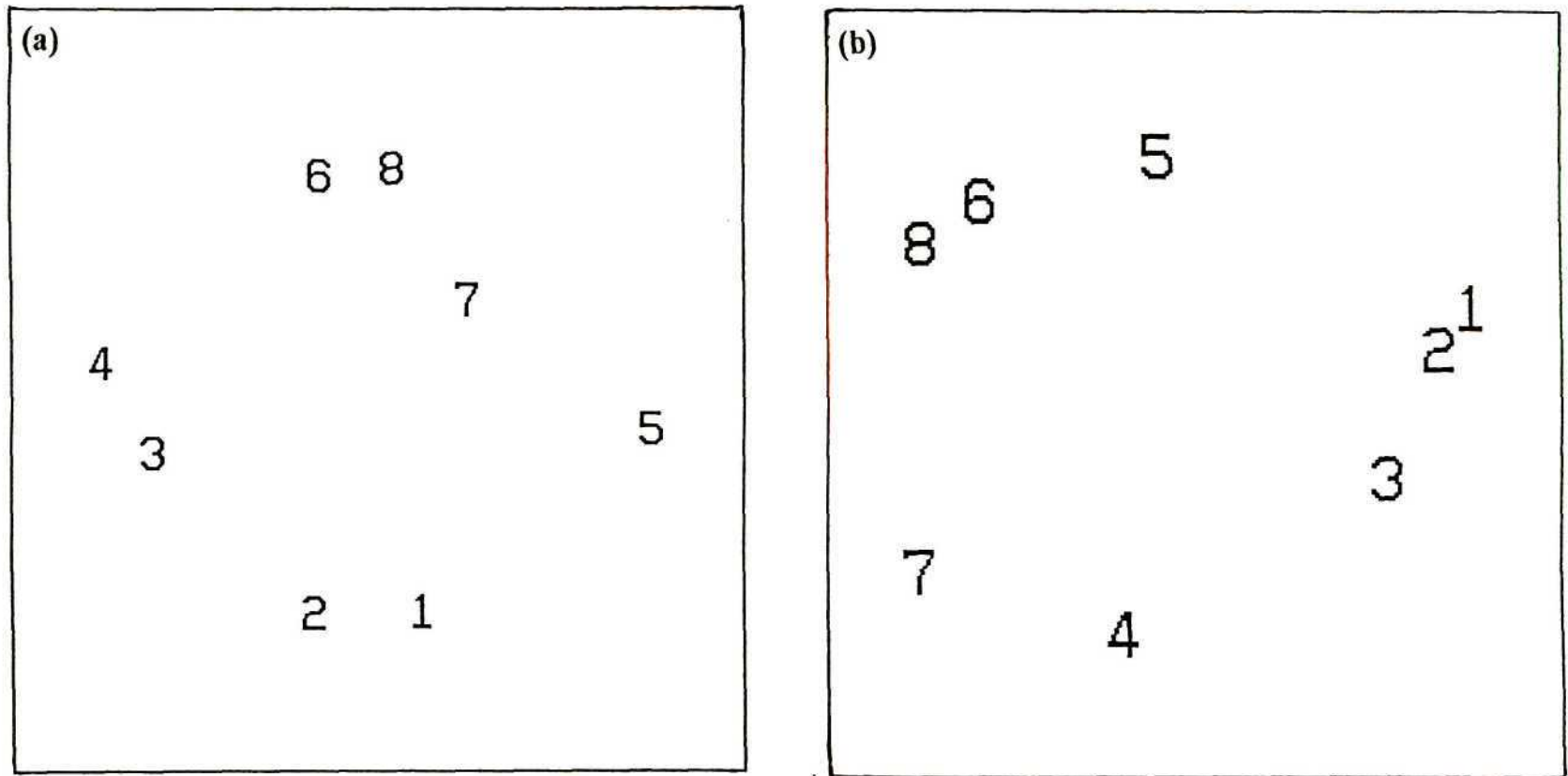


Figure 4.13: (a) A 2-dimensional PCA ordination of the 17 environmental variables listed in Chapter 3, section 3.3.4, and shown for the eight sites (1-8). Total variance explained by the first two components is 57%. (b) MDS ordination based on species data (biota).

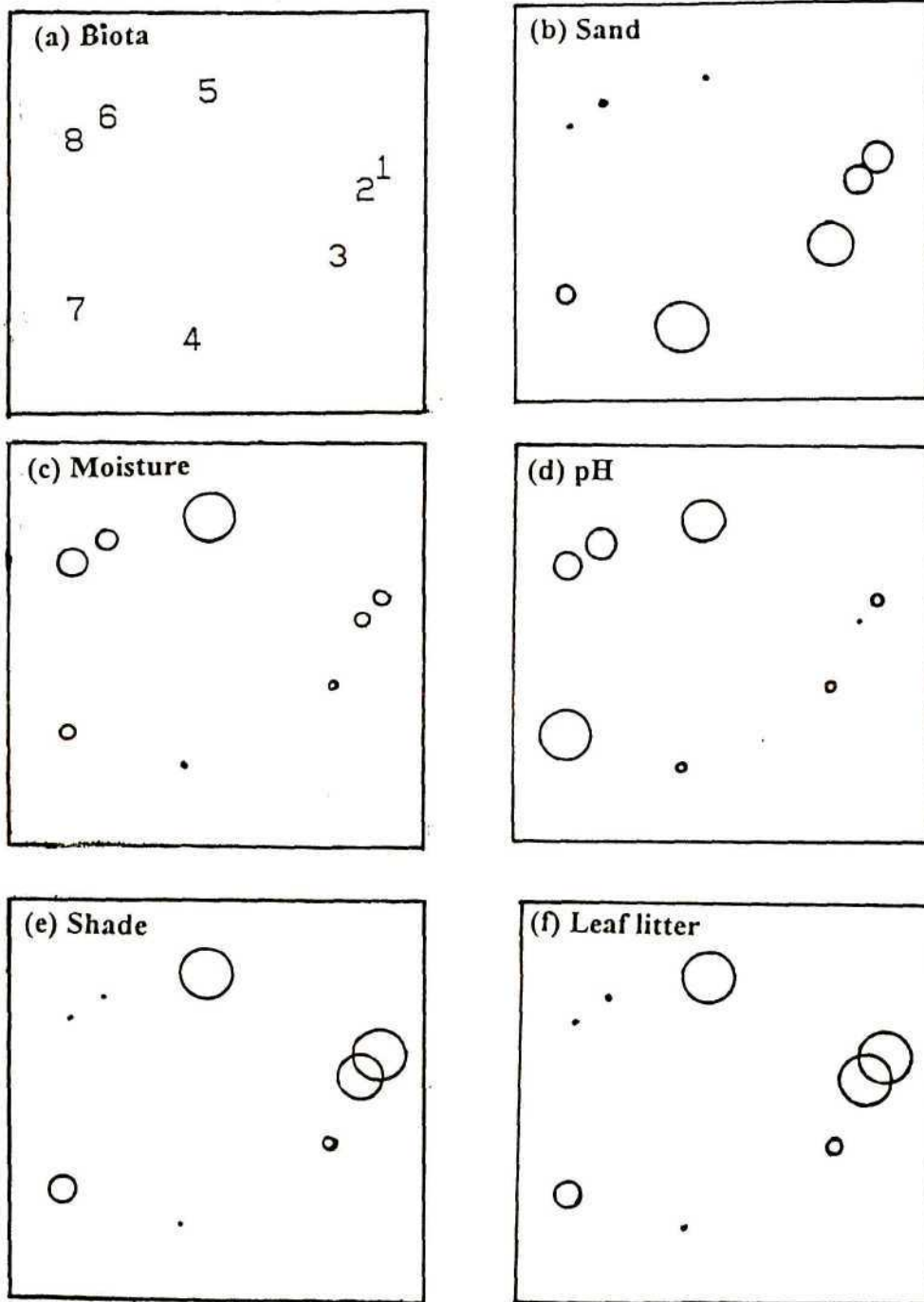


Figure 4.14: (a) MDS ordination of carabid and cicindelid species data (biota) of the eight sites (1-8). (b)-(f) is the same MDS but with superimposed circles of increasing size with increasing sand, moisture, pH, shade and litter as quantitative variables at each of the eight sites. Nominal variables specifying a classification of the eight sites are shown in (g) geographical location, (h) habitat type and (i) management regime.

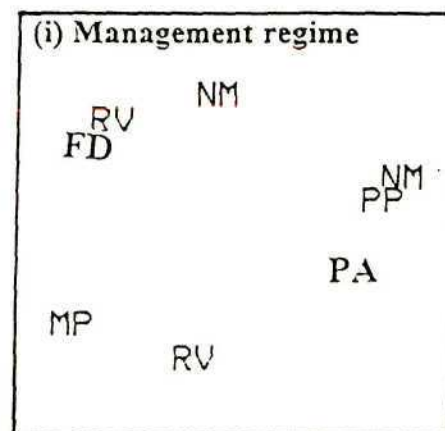
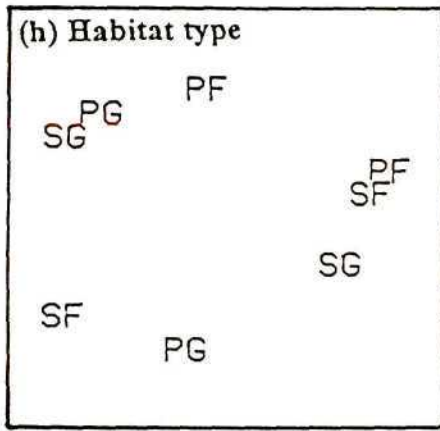
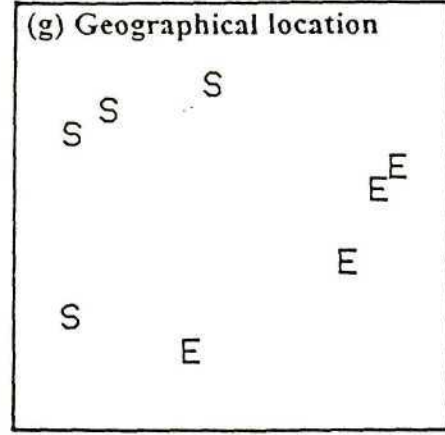
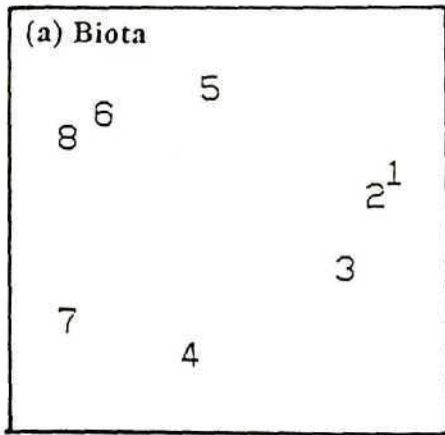


Figure 4.14: continued

road verge at S6 in the Savannah Zone after the site had been burnt. But it was never recorded at this site again in the following season after the grass had grown again. Therefore the amount of sand in A1 horizon and the vegetation type as short grass induced by burning or cutting influences the choice of preferred habitat of these cicindelids.

Fig. 4.14d, shows that, the soil pH of sites (S5, S6, S7, S8) in the Savannah Zone were more basic and soils at higher altitude in the Escarpment zone (S1, S2, S3, S4) were more acidic, resulting in a pH gradient from high to low altitude. Shade and leaf litter are very strongly correlated giving very similar patterns (Fig. 4.14 e-f), and no gradients are shown based on altitude.

Fig. 4.14(g-I), are the nominal variables of geographic location or altitude, habitat type and land use or management regimes respectively.

In Fig. 4.14g, one can clearly see the separation of sites in the Savannah Zone (S) from those in the Escarpment Zone (E). This factor of altitude plays a role in determining the carabid and cicindelid species abundance patterns created by the MDS ordination, in addition to the soil characteristics of sand in the A1 horizon (Fig. 4.15b) and soil pH (Fig. 4.15c) which gave similar patterns to that of altitude.

The nominal variable 'Habitat type', was based on a classification of whether a particular site's vegetation was primary grassland (PG), secondary grassland (SG), primary forest (PF), or secondary forest (SF). The nominal variable 'management regime', was based on the type of land-use at each site namely, nature management (NM), pine plantation (PP), park (PA), road verge (RV), macadamia plantation (MP) and a grassland field of hay (FD). One can clearly see in Fig. 4.14 (h) and (I) that soil characteristics as sand, pH, moisture in (Fig. 4.14b, c, d), and geographical location (Fig. 4.14g) still play a greater role in grouping sites than habitat type and type of land-use management regimes. There are no gradients based on these variables.

4.7.1.3.3 Linking species patterns to multivariate environmental variables

The intuitive premise adapted here is that if the suite of environmental variables responsible for structuring the community were known, then samples having similar values for these variables

would be expected to have rather similar species composition, and an ordination would group sites in the same way as for the biotic plot. If key environmental variables are omitted, the match between the two plots will deteriorate. In the same way, the match becomes worse if abiotic data which are irrelevant to the community structure are included.

First the importance of individual environmental variables was determined. Fig. 4.15a, being an MDS ordination plot of the eight sites based on species abundance data, was compared with MDS plots (Fig. 4.15b-I), based on individual environmental variables and the grouping of sites compared to see if the patterns matched.

It was clear that, MDS ordinations based on sand, pH and geographical location or altitude as in (Fig. 4.15b, c, g), are the only environmental variables that match the biotic MDS ordination. The other variables, litter, shade, habitat type and management regime (Fig. 4.15e, f, h, I) on their own, tend to distort the biotic pattern. The variables, leaf litter and shade gave similar patterns (Fig. 4.15e, f), and therefore one of them was irrelevant.

The moisture pattern (Fig. 4.15d), had macadamia plantation (S7), in the Savanna Zone under intensive irrigation placed closer to site S1, an indigenous forest and a pine plantation (S2) which receive high annual rainfall and were cooler compared to S5, S6 and S8 in the hot and dry savanna climate. Otherwise, the moisture pattern matched the species data.

Therefore, the quantitative variables of soil characteristics, sand, pH and moisture and the nominal variable, geographical location (altitude) each of which contributed substantially to explaining species patterns.

Secondly, determination of combinations of environmental variables that best explain the community structure was carried out. Quantifying the match between any two plots was done by taking the ranks for the Bray-Curtis similarity matrix for biota and the Euclidean distance matrix for environmental variables and comparing them through a weighted Spearman rank correlation coefficient (ρ_w) (Kendall, 1970). Spearman rank correlation coefficient (ρ_w) lies in the range -1 to 1, where the two sets of ranks are in complete opposition or complete agreement. Values of ρ_w around zero correspond to the absence of any match between the two patterns. The computer

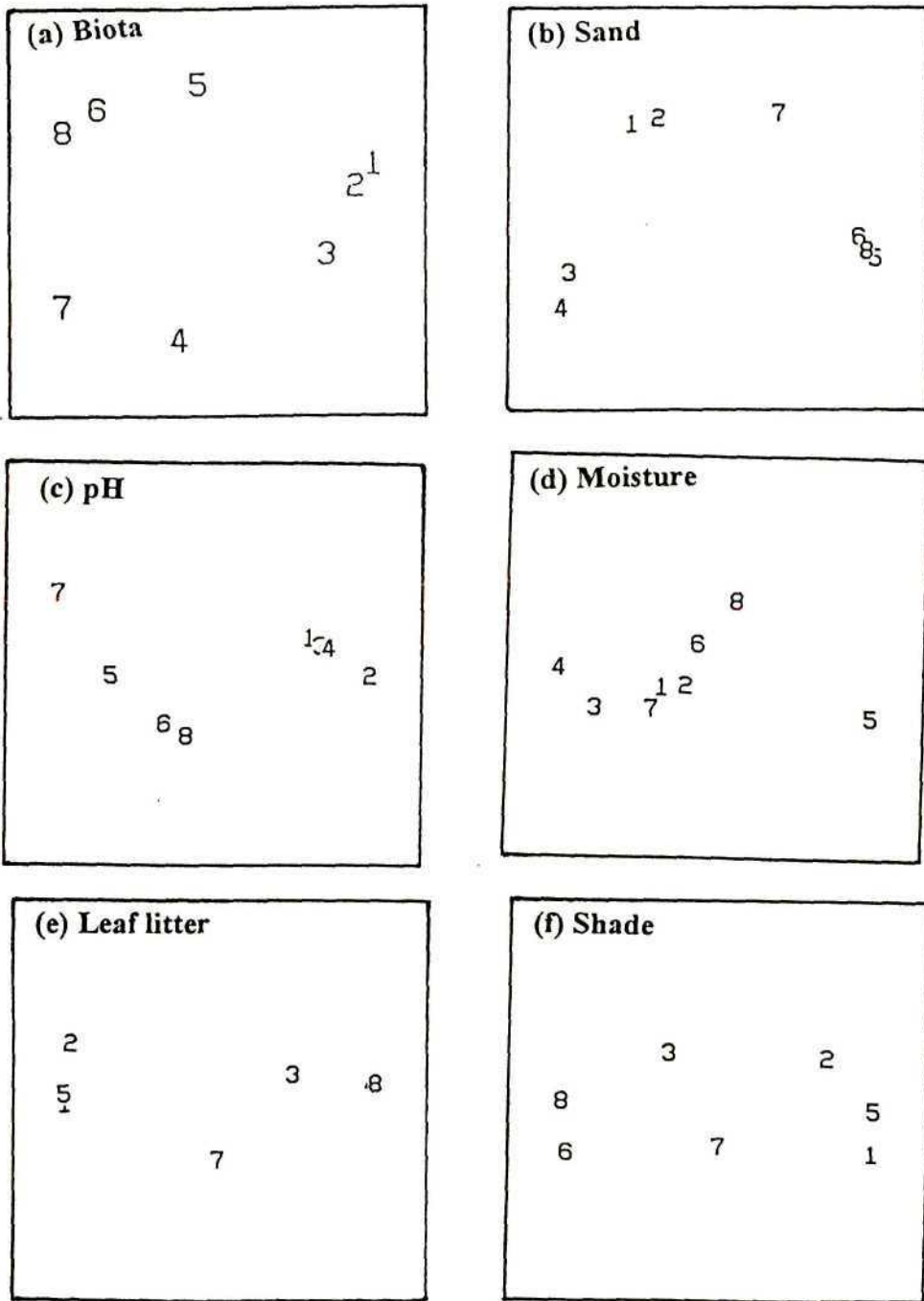


Figure 4.15: (a) MDS ordination of carabid and cicindelid species data (biota) of the eight sites (1-8). (b)-(f) MDS ordination based on sand, pH, moisture, litter and shade as quantitative variables. MDS ordination based on nominal variables specifying a classification of the eight sites shown as, (g) geographical location, (h) habitat type and (i) management regime.

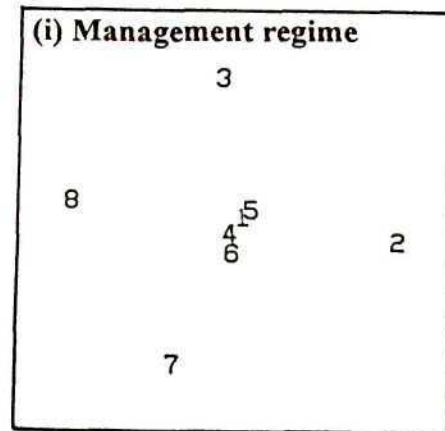
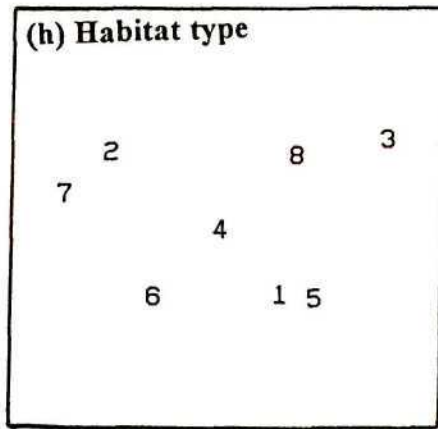
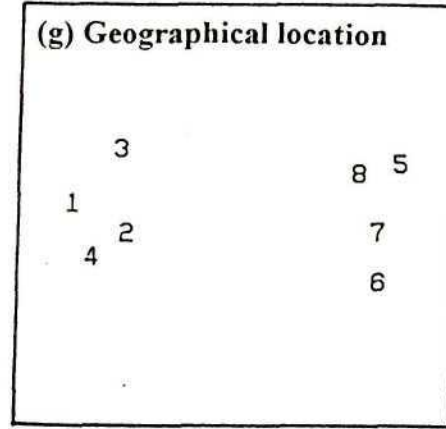
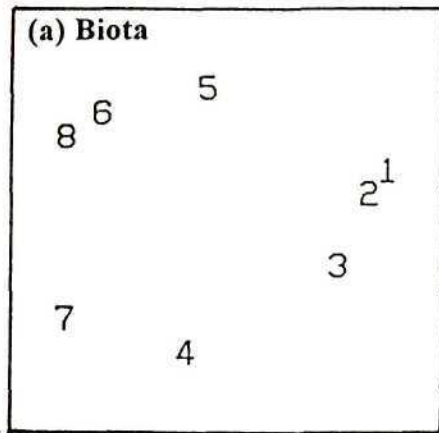


Figure 4.15: continued

program BIO-ENV in PRIMER was used to carry out this test.

Table 4.34 gives combinations of the eight environmental variables, taken k at a time and the resulting weighted Spearman rank correlation value (ρ_w) that measures the degree of matches of biotic and abiotic similarity matrices. Combinations of various soil characteristics of sand, pH, moisture and litter at the k2 and the k3 level gave rise to a maximum correlation value of 0.410 with combinations of sand, pH and fallen leaf/twig litter. Dropping the variable 'moisture', did not change this correlation value. Dropping the variable 'litter', decreased this value (0.410-0.387) by 23 units. Dropping the variable 'sand', decreased the correlation value by 113 units and dropping the variable 'pH', decreased the correlation value by 122 units.

Therefore the order of importance of the soil characteristics in explaining species data was pH, sand, litter and moisture. This information is seen graphically in (Fig. 4.16a), which shows MDS ordination based on biota and some of the MDS ordinations of environmental variable combinations from Table 4.34 and shown in (Fig. 4.16c-I). Presence of combinations of soil characteristics alone at the k3 and k4 level was adequate in separating the eight sites along geographical location or altitude where sites at high altitude (S1, S2, S3, S4) were grouped on one end of the diagram and those at lower altitude (S5, S6, S7, S8) were grouped on the opposite side of the diagram e.g. (Fig. 4.16c).

Addition of the nominal variable, geographical location or altitude, to soil characteristics, increased the Spearman rank correlation from (0.454 to 0.498) by +4 units and the respective ordination diagram showed a distinct separation of sites based on altitude (Fig. 4.16d).

Addition of the nominal variable, habitat type, to soil characteristics decreased the rank correlation value from (0.454 to 0.421) by -33 units. However the resulting MDS diagram still matched species patterns. But this was due to the presence of soil characteristics in the ordination, (Fig. 4.16e).

Addition of the nominal variable management regime to soil characteristics, increased the rank correlation value from (0.454 to 0.494) by +40 units and the resulting MDS ordination (Fig. 4.16f) matched the species patterns as the sites were separated along geographical location.

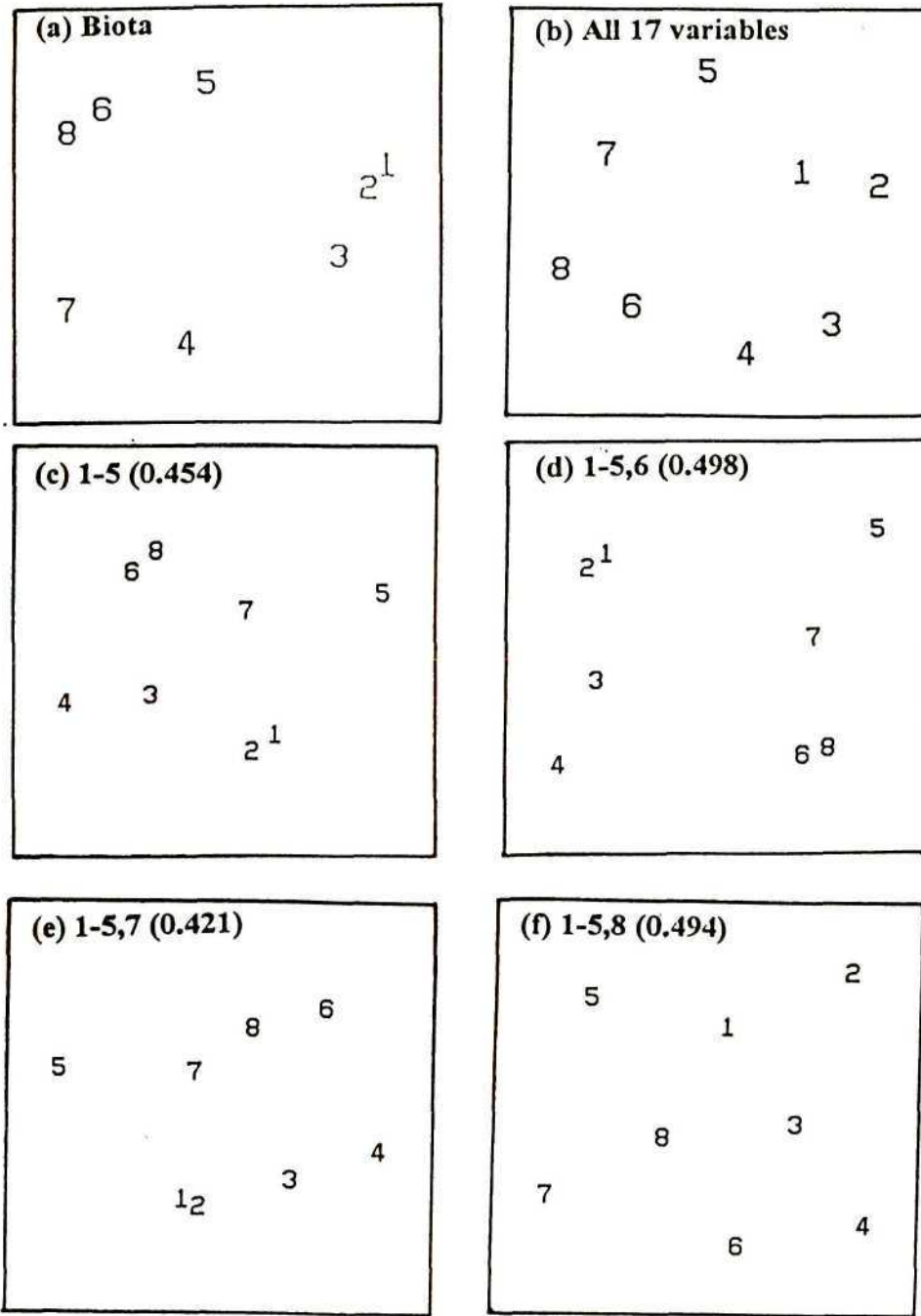


Figure 4.16: (a) MDS ordination of carabid and cicindelid species data (biota) of the eight sites (1-8). (b) is PCA of all 17 environmental variables listed in Chapter 3, section 3.3.4. (c)-(i) MDS ordination based on combinations of environmental variables listed in section 3.3.4 as sand, pH, moisture, litter and shade (1-5); geographical location (6), habitat type (7); management regime (8). Numbers in brackets are Spearman's rank correlation values ρ_w .

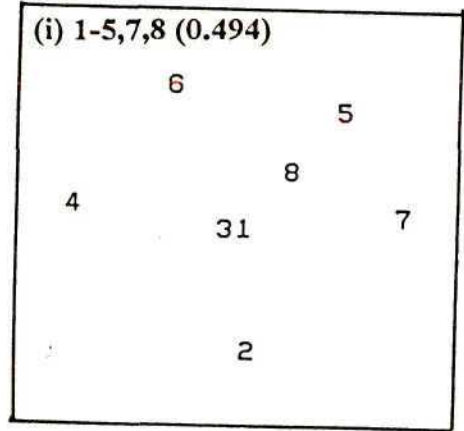
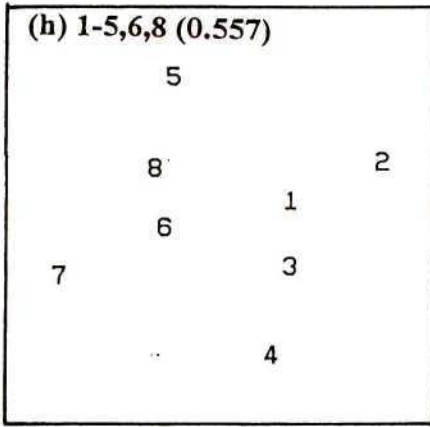
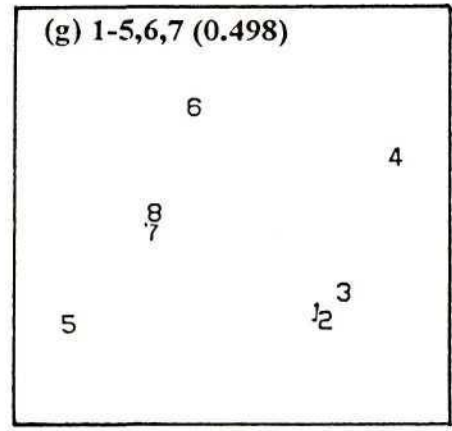
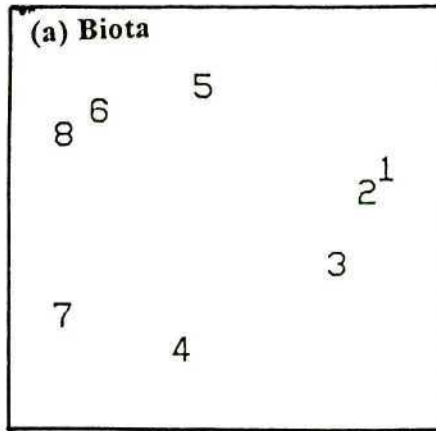


Figure 4.16: continued

	GROUP (Sites)	AVERAGE SIMILARITY	AVERAGE DISSIMILARITY	DISCRIMINATING SPECIES (code numbers)
1	1 and 2	63.38	-	
2	6 and 8	64.85	-	
3	3 and S1 & 2	-	48.18	45a, 150, 155
4	4 and S1 & 2	-	79.92	032, 250a, 014, 250b, 150, 181, 178, 126, 40b
5	4 and 3	-	70.72	
6	5 and S1 & 2	-	73.00	243, 032, 105, 256, 35b, 240b, 250a
7	5 and 3	-	66.71	
8	5 and 4	-	75.08	
9	7 and S1 & 2	-	82.59	126, 150, 032, 133, 130b, 178, 154, 257, 276, 256, 40a
10	7 and 3	-	74.15	
11	7 and 4	-	71.20	
12	7 and 5	-	76.40	
13	6 & 8 and 1 & 2	-	82.86	032, 252, 140
14	6 & 8 and 3	-	79.93	115a, 032, 45a, 147, 140, 155, 150, 254, 35a
15	6 & 8 and 4	-	67.42	115a-w, 115a, 240a, 007, 014, 150, 250b, 181, 40b
16	6 & 8 and 5	-	62.29	105, 115a, 256, 240b, 35b, 35a, 147, 130a
17	6 & 8 and 7	-	69.97	150, 115a, 35a, 130b, 154, 257, 147, 256, 275, 40a

Table 4.33: Species determining the observed sample (site) patterns, i.e. good discriminators of groups produced by cluster analysis (Fig. 4.9), and MDS analysis (Fig. 4.10). These results were obtained using the program *simper* (similarity percentages) in *PRIMER*, which calculates contribution from each species to the separation of pairs of clusters as average similarity within a group and average dissimilarity between groups. Species are shown as code numbers in column five, refer to Table 4.1 for actual names of species.

	Environmental Variable Combinations (pw)							
K1	1, Sand (0.228)	2, pH (0.245)	3, Moisture (-0.056)	4, Litter (0.230)	5, Shade (0.195)	6, Geographical location (0.454)	7, Habitat type (0.225)	8, Management regime (0.324)
K2	1, 4 (0.288)	3, 4 (0.230)	2, 3 (0.245)	2, 4 (0.297)	1, 2 (0.387)			
K3	2, 3, 4 (0.297)	1, 2, 3 (0.387)	1, 2, 4 (0.410)					
K4	1 - 4 (0.454)							
K5	1 - 5 (0.454)	1 - 4, 7 (0.421)	1 - 4, 8 (0.494)	1 - 4, 6 (0.498)				
K6	1 - 5, 7 (0.421)	1 - 5, 8 (0.494)	1 - 5, 6 (0.498)					
K7	1 - 5, 7, 8 (0.494)	1 - 5, 6, 7 (0.498)	1 - 4, 6, 8 (0.557)	1 - 5, 6, 8 (0.557)				
K8	1 - 5, 6, 7, 8 (0.557)							

Table 4.34: Combinations of eight environmental variables listed in the second row (K1), taken at level K1 (individually) to K8 (combinations of eight variables e.g 1-5,6,7,8), and the resulting weighted Spearman rank correlation value *pw* shown in brackets, that measures the degree of matches between biotic and abiotic similarity matrices. Bold type indicates overall optimum match. Bio-env in *PRIMER* was used.

Addition of the nominal variables, geographical location and management regime to soil characteristics, increased the correlation value from (0.454 to 0.557) by +103 units (Fig. 4.16h). This was the overall optimum combination that gave the highest Spearman rank correlation value (0.557) and that best matched the species patterns at the k7 level, with combinations of soil characteristics in order of importance as: pH, sand/moisture, litter and the nominal variables of management regimes and altitude. It should be noted that, the variables sand and moisture are negatively correlated in a soil, hence when the variable moisture was omitted from the analysis, the resulting spearman rank correlation value was not affected. Likewise, the variable altitude appears to have little effect here because the underlying soil characteristics of pH and moisture form altitudinal gradients across the two geographical regions under study.

Omission of the environmental variable, shade from the analysis did not affect the Spearman rank correlation value as shade and litter were found to be highly correlated.

The variable 'habitat type', that characterized sites based on whether the landscape was a primary or secondary grassland or forest had little effect in determining species patterns as can be seen from the resultant Spearman rank correlation values (Table 4.34).

4.7.2 Ordination of species using CANOCO

4.7.2.1 Ordination (CA and CCA) at the landscape level

4.7.2.1.1 CA at the landscape level using species data of two seasons

Correspondence analysis (CA) was first carried out with square-root transformed species data to down-weight high abundances and to extract from the species data, the dominant pattern of variation in community composition among the eight sites without any environmental variables.

DCA was also carried out on the same data with square-root transformed species data to down weight high abundances and it was found to give the same information as CA with square-root transformed data. When untransformed data was used in CA, the subsequent ordination diagram displayed had very few species and did not give as much information as that with transformed data. Therefore, CA was used.

Fig. 4.17 is the CA ordination diagram displaying the species and site points. The four forest and four grassland sites situated at high and low elevation clearly break down into six groups. See Table 4.1 for full names of species. The numbers allocated to species in the diagram (Fig. 4.17) are default numbers given to species by CANOCO, according to the order of species listing in Table 4.23 Appendix 2. From the species and site points in the ordination diagram (Fig. 4.17), it can be inferred that in the right-hand side of the diagram, S1, S2 and S3 are closer to each other and therefore more similar as they share many species. These sites are all situated at high altitude.

Species exclusively common to the indigenous forest (S1) and the adjacent pine plantation (S2) and the park (S3) within the Escarpment zone as shown in (Fig. 4.17) were, *Craspidophorus bonvouloiri* (003), *Cophosomorpha pseudocastellani* (005), *Lebiini* sp.(002), *Metaxinidium nanum* (011), *Systolocranius alternaris* (004), *Stenodinodes fenestratus* (010) and *Lebia* sp.155 (032). Specifically, *C. bonvouloiri* (003) and *C. pseudocastellani* (005) were recorded in the natural indigenous forest at S1 and the pine plantation at S2, *M. nanum* (011) occurred in the three sites, (S1, S2 and S3) and *S. fenestratus* (010) and *Lebia* sp. 155 (032) in the Park (S3).

The species situated in the centre of the diagram (Fig. 4.17) were largely eurytopic. Specifically, Pterostichini species, *Metagonum gilvipes* (115a) was mainly recorded in forest sites at, (S1, S2, S5, S7) situated both at high and low altitude. This species was also recorded in the grassland habitats of S3 and S4 but higher abundances were at point habitats that were near trees that provided shelter and leaf litter namely point habitat numbers 11 and 16 (Table 4.26). Harpalini sp. (35a) (009), was common to all sites except the forests at S1 and S7. The *Lebiini* species, *Hystrichopus atratus* (007) was common in forests under nature management both at high and low altitude (S1 and S5), it was also present the macadamia plantation (S7) under agricultural management. The *Lebiini* species common in forests under nature management both at high and low altitude (S1 and S5) was *Lebia insidiosa* (130a).

Species in the bottom left-hand corner of the diagram (Fig. 4.17) were dominant in sites (S5, S6, S7 and S8), situated at lower altitude of the savanna zone. Specifically, *Hystrichopus mnischechi* (024) was recorded only at S5. *Pachydinodes bipustulatus* (029) was common at S5 and S7. Carabidae sp. 243 (023) reached maximum abundance at S5, but was also recorded at S6 and S8. *Hyparpalus*

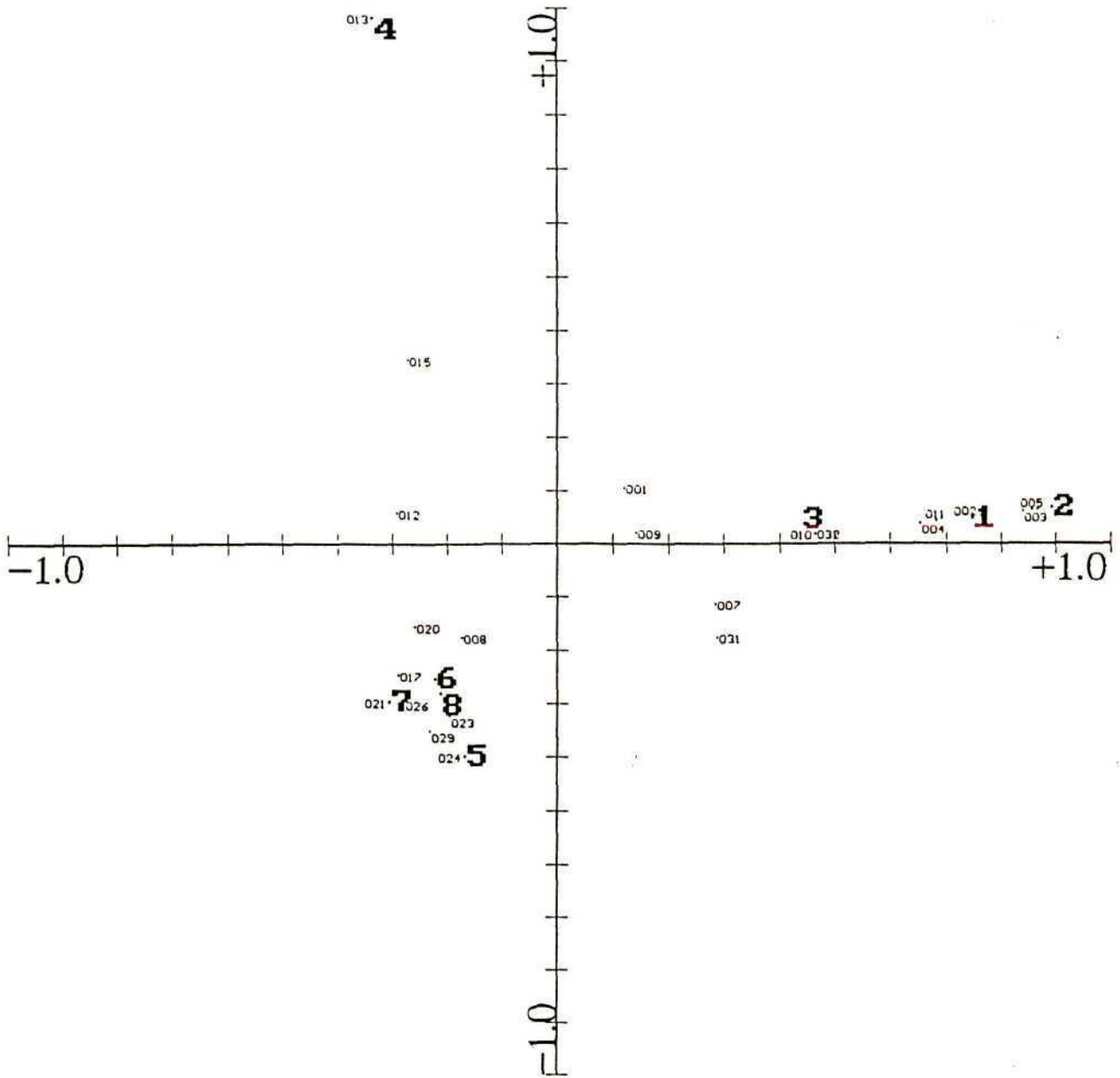


Figure 4.17: Ordination diagram of correspondence analysis (CA), using carabid and cicindelid species data as sum of two sampling seasons, June 1994-May 1996 (Table 4.23). The first axis $\lambda_1=0.691$ is horizontal and the second axis $\lambda_2=0.620$ is vertical. The diagram shows the distribution of species among the eight sites (1-8 shown in bold type numbers). Species are shown in small type numbers following the order of listing in Table 4.23. CANOCO was used.

tomentosus (133), *Chlaeniostenus. cylindricus* (021), *Harpalini sp.* (126)(017), *Harpalini sp.* (115b) (008), *Harpalini sp.* (150)(020) and *Callistomimus caffer* (012) reached maximum abundance in site S7.

In the top left-hand corner of the diagram (Fig. 4.17), S4 was placed on its own as a unique habitat having many species that were different from those found at other sites. Although S4 was situated at high altitude, it was dissimilar to S1, S2 and S3. The effect of altitude was minimised and the burning disturbance contributed a lot to this distribution pattern. *Dromica gilvipes* (015) was recorded in the road verge landscape element of S4 and S6 with maximum abundance in S4.

These inferences from the diagram agree with the data (Table 4.23 Appendix 2). However not all species have been represented, only the most abundant and those unique to a site or rather the discriminating species have been shown due to space availability.

In Fig. 4.17, the cumulative % variance for the first axis ($\lambda_1=0.691$) and second axis ($\lambda_2=0.620$) was 51.8% (Table 4.35).

4.7.2.1.2 CCA at the landscape level using species data of two seasons

To explain the main pattern of variation in the species data. CCA was carried out to relate the 17 environmental variables (see section 3.3.4) to species data. These number of variables is too large to sort out their independent effects on community composition. If the highest number of environmental variables (q) is greater or equal to $n-1$, where n is the number of samples, then CCA is then just CA (Jongman *et al.*, 1987). To avoid this problem, CCA was carried out with combinations of various environmental variables to determine which combination best matched the species data as shown in the CA diagram in Fig. 4.17.

4.7.2.1.2(a) CCA based on combinations of environmental variables related to soil characteristics

Fig. 4.18 is a display of the CCA ordination results carried out to investigate the differences in the distribution patterns of carabids and cicindelids among the eight sites based on environmental variables related to soil characteristics, namely, variables 1-5 in section 3.3.4 being sand, pH, moisture, leaf/twig litter, and shade. The computer program CANOCO detected multicollinearity

between shade and litter, as they had very high variance inflation factors (VIF). Shade was therefore omitted from the analysis and this had no effect on the subsequent ordination diagram produced (Fig. 4.19). However, when this pattern was compared to that produced by CA (Fig. 4.17), it can be seen that S4 and S3 have now been brought closer together. Detailed results of this analysis are listed in Table 4.35.

The first axis ($\lambda_1=0.672$) separates sites that have soils with very high pH, i.e. less acidic (S7, S5, S6, S8) from those with lower pH, i.e. more acidic (S2, S4, S3, S1). The pine plantation (S2) was very acidic and the macadamia plantation (S7) was more basic. The second axis ($\lambda_2=0.559$) is that of sand and moisture, where sites with high sand content had soils which hold less moisture (S4 and S3). These sites were separated from those with soils that had less sand content and hold more moisture. S5 had the highest soil moisture due to its high clay content.

To investigate whether the observed differences could be accounted for by pure chance, the Monte Carlo permutation test with the first eigenvalue as test statistic was carried out which yielded a probability value $P=0.02$. It is therefore concluded that, there are significant differences in the distribution patterns of carabids and cicindelids among the eight sites based on soil characteristics and that these soil characteristics are important in determining these patterns.

Further analyses were carried out to determine which combinations of the four soil characteristics were very important in determining the distribution patterns of these animals. Results of combinations of CCA with various combinations of the four soil characteristics can be seen in Table 4.35. Dropping the environmental variable 'sand' in the A1 horizon reduced the first eigenvalue produced with (1-4) environmental variables together by only six units. The subsequent ordination diagram produced was very similar to that of Fig. 4.19 with all the four soil characteristics. The first canonical axis was significant ($P=0.02$) and separated sites with high leaf/twig litter from those with high pH values. When the variable soil moisture was dropped from the analysis, 15 units were reduced and the first canonical axis that separated sites with high sand content from those with high pH was significant ($P=0.02$). Removing 'leaf litter' from the analysis, 51 units were reduced and the first canonical axis of sand and pH was not significant ($P=0.16$). Finally, removing pH from the analysis, 115 units were reduced and the first canonical axis of sand and moisture was not

Type of analysis: Season data and combinations of Environmental variables for CCA	First axis and second axis eigenvalue s (λ)	Species- environme nt correlatio ns	Cumulative (%) variance of species data	Cumulative (%) variance of species- environmental relations	Inter-set correlations shown as gradients	Monte-Carlo significance tests (P)	
						First axis	Overall test
CA (94-96) landscape level	1st 0.691	-	27.3				
	2nd 0.620	-	51.8				
CCA (94-96) 1-5	1st 0.675	0.996	26.7	31.9	sand - pH	P = 0.06	P = 0.02**
	2nd 0.565	0.966	49.0	58.7	sand - moisture		
CCA (94-96) 1-4	1st 0.672	0.996	26.5	35.4	sand - pH	P = 0.02**	P = 0.04*
	2nd 0.559	0.967	48.6	64.8	sand - moisture		
CCA (94-96) 2, 3, 4	1st 0.666	0.997	26.3	43.7	litter - pH	P = 0.01***	P = 0.05*
	2nd 0.514	0.939	46.6	77.4			
CCA (94-96) 1, 2, 3	1st 0.657	0.991	26.0	44.7	litter - pH	P = 0.02**	P = 0.05*
	2nd 0.557	0.965	48.0	82.7			
CCA (94-96) 1, 2, 3	1st 0.621	0.988	24.5	43.8	sand - pH	P = 0.16	P = 0.10
	2nd 0.504	0.928	44.4	79.3			
CCA (94-96) 1, 3, 4	1st 0.557	0.978	22.8	39.3	sand - moisture	P = 0.37	P = 0.07
	2nd 0.466	0.891	41.2	71.1			
CCA (94-96) 2, 4	1st 0.657	0.990	25.9	61.8	litter - pH	P = 0.01***	P = 0.10
	2nd 0.406	0.881	42.0	100.0			
CCA (94-96) 1, 2	1st 0.621	0.988	24.5	42.4	sand - pH	P = 0.05*	P = 0.07
	2nd 0.454	0.905	57.8	100.0			
CCA (94-96) 8-11	1st 0.503	0.926	19.9	49.1	PG -SF PF - PG	P = 0.66	P = 0.58
	2nd 0.371	0.857	34.5	85.2			
CCA (94-96) 12-17	1st 0.641	0.989	25.3	35.4	PP - MP RV - MP	P = 0.37	P = 0.38
	2nd 0.502	0.920	45.1	63.1			
CCA (94-96) 12-17, 6	1st 0.658	0.994	26.0	49.4	E - MP NM - E	P = 0.53	P = 0.10
	2nd 0.593	0.995	28.8	54.8			
CCA (94-96) 2-4, 12, 15, 16	1st 0.689	0.999	27.2	29.5	litter - pH RV - NM	P = 0.03**	P = 0.05*
	2nd 0.618	0.999	51.6	56.0			
CA (94-95) landscape level	1st 0.764	-	27.7				
	2nd 0.575	-	48.5				
CCA (94-95) 2-4, 12, 15, 16	1st 0.750	0.996	27.2	31.0	litter - pH NM - MP	P = 0.13	P = 0.20
	2nd 0.571	0.999	47.9	54.7			
CA (95-96) landscape level	1st 0.737	-	25.0				
	2nd 0.688	-	48.4				
CCA (95-96) 2-4, 12, 15, 16	1st 0.736	1.000	25.0	27.2 51.6	RV - moisture NM - MP	P = 0.1	P = 0.03**
	2nd 0.662	0.999	47.5				
CA (94-96) point habitat level	1st 0.735	-	17.0				
	2nd 0.678	-	32.7				
PCA (94-95) point habitat level	1st 0.583	-	58.3				
	2nd 0.108	-	69.0				
CA (95-96) point habitat level	1st 0.823	-	15.0				
	2nd 0.788	-	29.4				

Table 4.35: Ordination results of CA (at the landscape level and at the point habitat level within sites) and CCA produced by running CANOCO, using species data as sum of two seasons (June 1994-May 1996), first sampling season (June 1994-May 1995) and second sampling season (June 1995-May 1996). Numbers 1-17 in the first column, are combinations of environmental variables listed in Chapter 3, Section 3.3.4. Highly significant gradients are shown with (***)

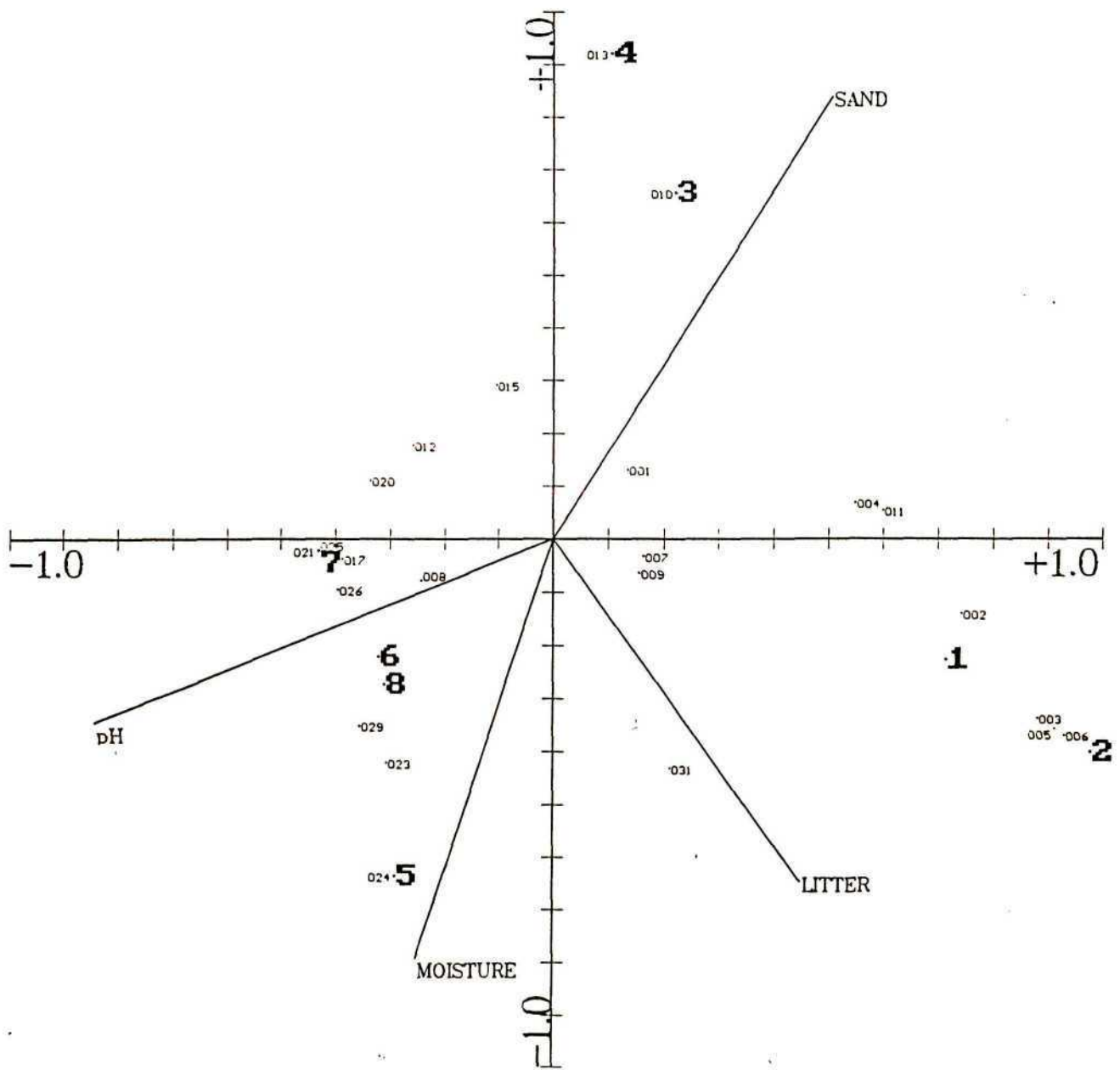


Figure 4.19: Ordination diagram of canonical correspondence analysis (CCA), using data as sum of two sampling seasons (June 1994-May 1996). It is based on four environmental variables of soil characteristics 1-4, listed in Section 3.3.4. The diagram shows the distribution of carabid and cicindelid species among the eight sites (1-8 in bold type numbers), and along environmental variable gradients (oblique axis). Species are in small type numbers following the order of listing in Table 4.23. The first axis $\lambda_1=0.672$ is horizontal and the second axis $\lambda_2=0.559$ is vertical.

significant ($P=0.37$). The ordination diagram produced did not match the species data at all, suggesting that soil pH was highly important.

Further, CCA with combinations of two environmental variables showed that only pH-litter and sand-pH produced significant first canonical axes. Removing sand and moisture from the analysis reduced the first axis by 15 units and the pH-litter axis was significant ($P=0.01$). Removing litter and moisture from the analysis reduced the first axis by 51 units and the sand pH axis was significant ($P=0.05$).

Therefore order of importance of soil characteristics in explaining species patterns is pH, litter, moisture/sand. These results show that although pH and fallen twigs and/or leaf litter as soil characteristics were found to be adequate in explaining species patterns, additional environmental variables sand and or soil moisture are necessary in giving a clearer picture as this factors are highly correlated in the environment.

4.7.2.1.2(b) CCA based on environmental variables related to soil characteristics and altitude

Addition of the nominal altitude variables, namely, 'Escarpment' and 'Savanna' to the (1-4) soil characteristics, produced ordination diagram (Fig. 4.20) that was very similar to that without the altitude variable (Fig. 4.19). The first canonical axis went up by only two units. To test whether the differences in the distribution patterns of carabids and cicindelids among the eight sites could be fully accounted for by (1-4) soil characteristics, whose effects are clear from (Fig. 4.19), or whether the variation that remains after fitting these four environmental variables is systematically related to altitude. To answer this question, a partial CCA was carried out with the four environmental variables as covariables and the nominal altitude variables 'Escarpment' and 'Savanna' as the variables of interest. The first eigenvalue of this analysis ($\lambda_1=0.169$) was subjected to the Monte Carlo permutation test and was not significant ($P=0.57$). Therefore the variation in the carabid and cicindelid distributions among the eight sites that remains after fitting the soil characteristics sand, pH, moisture and litter was not significantly related to altitude. In conclusion, the underlying pH and moisture gradients of the soil characteristics across this altitudinal gradient were sufficient to explain the carabid and cicindelid distributions among the eight sites.

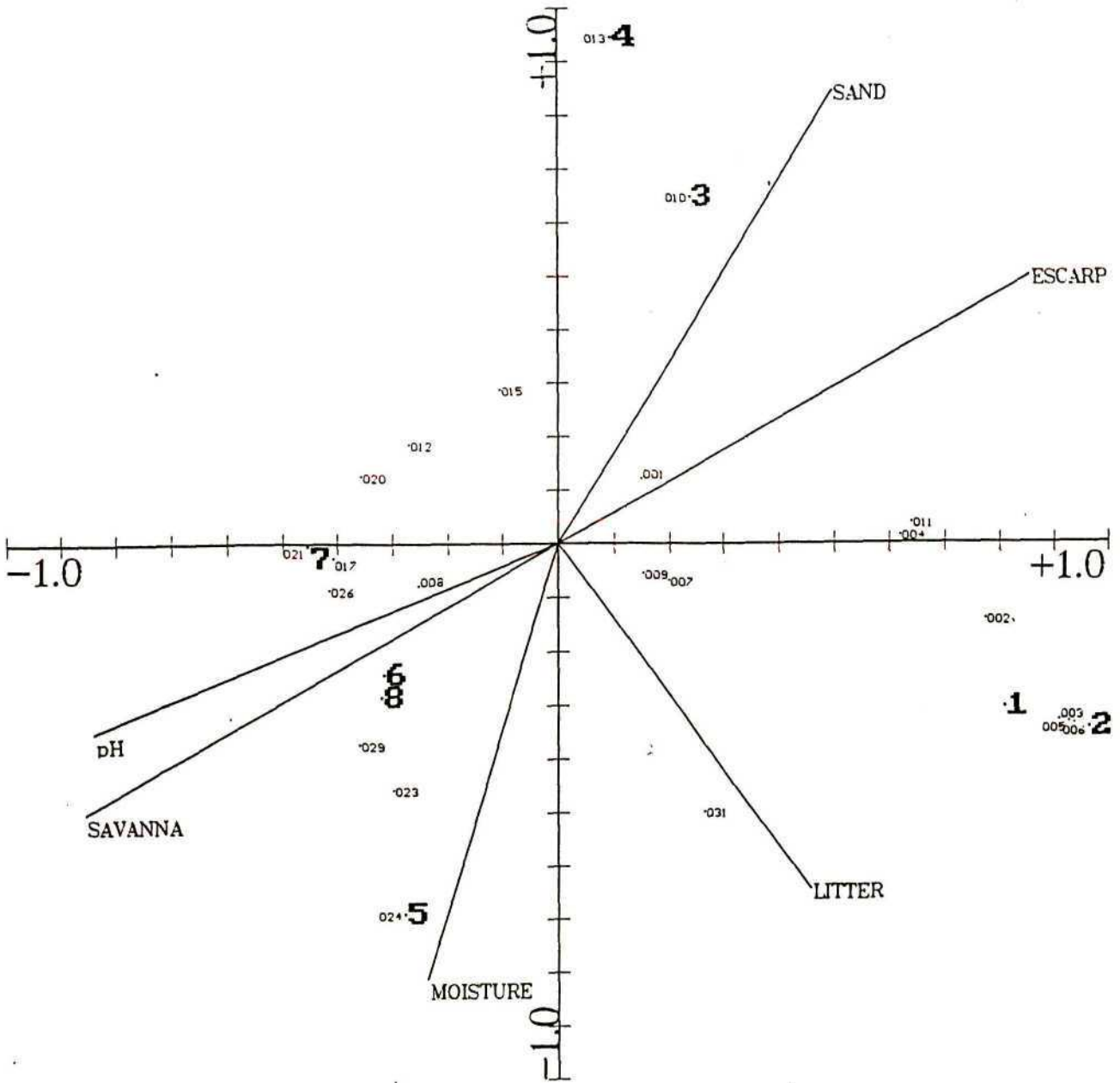


Figure 4.20: Ordination diagram of canonical correspondence analysis (CCA), using data as sum of two sampling seasons (June 1994-May 1996). It is based on environmental variables of soil characteristics 1-4 and geographical location 6-7, listed in Section 3.3.4. The diagram shows the distribution of carabid and cicindelid species among the eight sites (1-8 in bold type numbers), and along environmental variable gradients (oblique axis). Species are in small type numbers following the order of listing in Table 4.23.

4.7.2.1.2(c) CCA based on environmental variables related to 'habitat type'

Fig. 4.21 is the CCA ordination diagram produced to investigate the differences in the distribution of carabids and cicindelids among the eight sites based on the variable, 'habitat type' that had four nominal variables 8-11 (section 3.3 4) which characterised the eight sites as primary forest-PF (8), secondary forest-SF (9), secondary grassland (10), primary grassland-PG (11).

The first axis ($\lambda_1=0.503$) is seen to separate the sites having primary grasslands (S4, S6) from secondary grasslands (S3, S8) and secondary forest (S7, S2) habitats. The second axis ($\lambda_2=0.371$) separates sites with primary forests (S1, S5) from the rest of the habitats. From the species and site points in the CCA ordination diagram (Fig.4.21), we infer for example that *Hystriehopus mniszzechi* (024) was recorded in sites S1 and S5 and *Hyparpalus tomentosus* (026), Harpalini sp. (017), Harpalini sp. (020) reached maximum abundance in sites S7 and S2. But these inferences from the diagram do not agree with the data (Table 4.23 Appendix 2).

To investigate further whether the observed differences could be accounted for by pure chance, Monte Carlo permutation test with the first eigenvalue ($\lambda_1=0.503$) as test statistic was carried out, which yielded $P=0.66$. It was therefore concluded that there are no significant differences in the distribution patterns of carabids and cicindelids among the eight sites with respect to the variable 'habitat type'. And that 'habitat type' alone cannot explain the distribution of carabid and cicindelid species among the eight sites. This result was further backed by the fact that the ordination diagram in Fig. 4.21 did not match that of Fig. 4.17 based on species data alone.

Further ordinations of combinations of variables of 'habitat type' with altitude and soil characteristics produced first canonical axes that were not significant. For example, 'habitat type' and altitude ($P=0.12$); for 'habitat type', altitude, sand, pH and moisture ($P=0.44$); for 'habitat type', altitude, pH and litter ($P=0.52$).

4.7.2.1.2(d) CCA based on environmental variables related to land-use or management regime

To investigate the differences in the distribution patterns of carabids and cicindelids among the eight sites with different management regimes or land uses namely, variables 12-17 in section 3.3.4 being nature management-NM (12), pine plantation-PP (13), park-PA (14), road verges-RV (15),

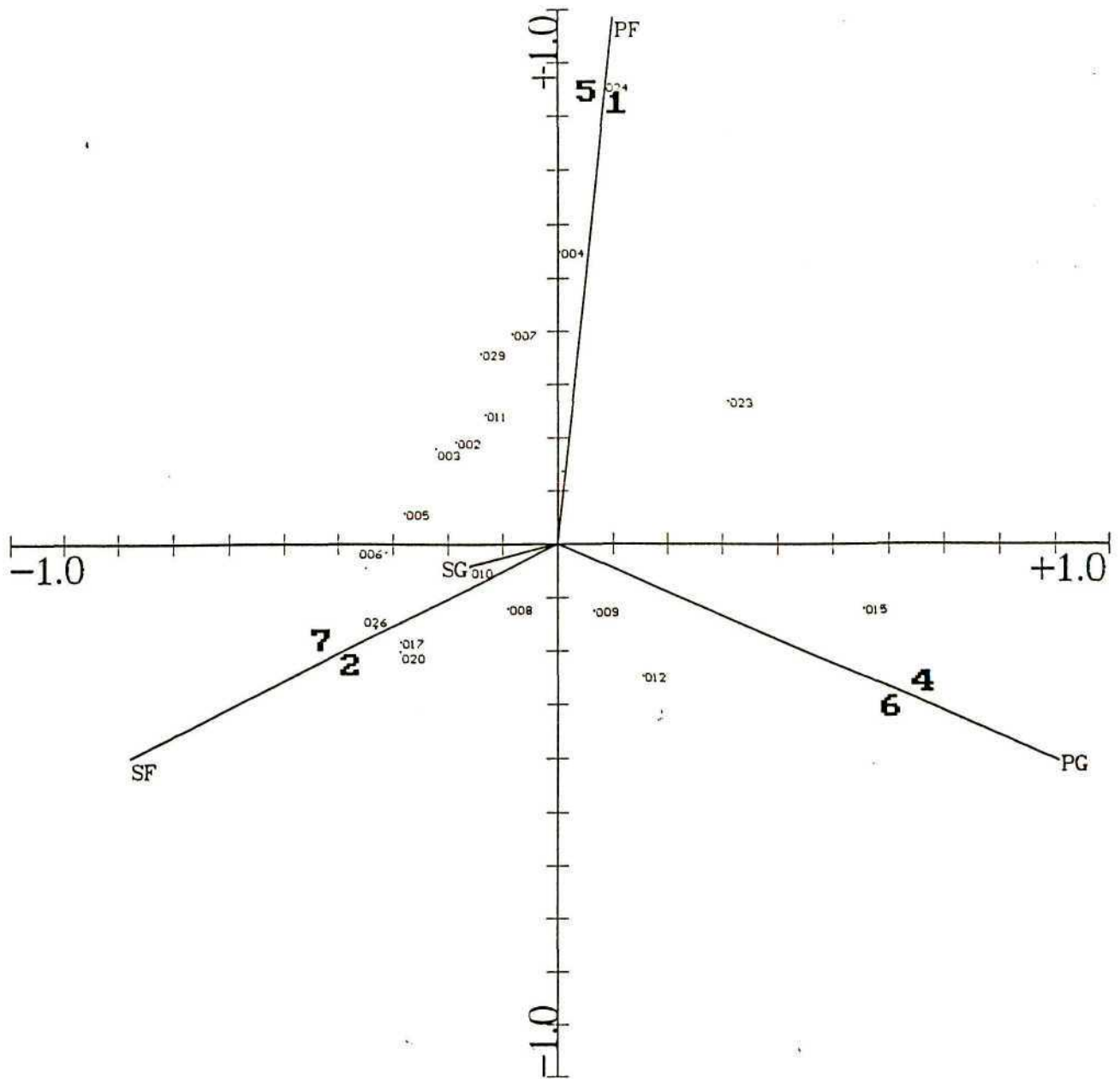


Figure 4.21: Ordination diagram of canonical correspondence analysis (CCA), using data as sum of two sampling seasons (June 1994-May 1996). It is based on environmental variables of habitat type 8-11, listed in Section 3.3.4. The diagram shows the distribution of carabid and cicindelid species among the eight sites (1-8 in bold type numbers), and along environmental variable gradients (oblique axis). Species are in small type numbers following the order of listing in Table 4.23. The first axis $\lambda_1=0.503$ is horizontal and the second axis $\lambda_2=0.371$ is vertical.

macadamia plantation-MP (16) and field-FD (17). Fig. 4.22 displays these differences.

The first axis ($\lambda_1=0.641$) is seen to separate pine plantation (S2) and nature management (S1, S5) and park (S3) from grassland fields (S8) and macadamia plantation (S7). The second axis ($\lambda_2=0.502$) separates road verges (S4, S6) from the rest. The natural reference classes were S2, S3, S7, and S8 and therefore species displayed in the vicinity of these sites agree with the data (Table 4.23 Appendix 2). The only species common to the two types of road verges at S4 and S6 was *Dromica gilvipes*. Although the sites with nature management have been grouped together (S1, S5), there was only one species, *Lebia insidiosa* (130a) that was exclusively recorded or common to these sites. The other species common to these two sites were eurytopic ones found in all the other sites as well e.g. *Metagonum gilvipes* (001), *Hystrichopus atratus* (007) and Harpalini sp. (008).

To test whether the observed differences can be accounted for by pure chance, Monte Carlo permutation tests with the first eigenvalue ($\lambda_1=0.641$) yielded $P=0.19$. It was therefore concluded that the different types of land uses or management regimes (on their own) among the eight sites cannot explain carabid and cicindelid species patterns. This can be visualized better by the differences between Fig. 4.22 and Fig. 4.17 with species data alone.

Addition of the variable altitude to various land-uses namely, NM, PP, RV, MP, (note that those not included in the analysis were merely reference classes and therefore did not affect the analysis), increased the first axis by 17 units ($\lambda_1=0.658$) but it was not significant $P=0.53$. The first axis was that of 'Escarpment' and 'Savanna' and the second axis separated sites with nature management from those of road verges. See details of results in Table 4.35.

4.7.2.1.2(e) CCA based on combinations of environmental variables

Various ordinations based on combinations of soil characteristics and land uses were carried out to determine which combinations best explained the species data. It was found that combinations of soil characteristics namely (pH, moisture, litter) and those of land-uses as (NM, RV, MP) gave the highest first axis eigenvalue ($\lambda_1=0.689$) which was significant ($P=0.03$) Fig. 4.23. The first axis separated sites with high leaf litter and twigs from those with high soil pH. The second axis separated sites with road verges from those with nature management.

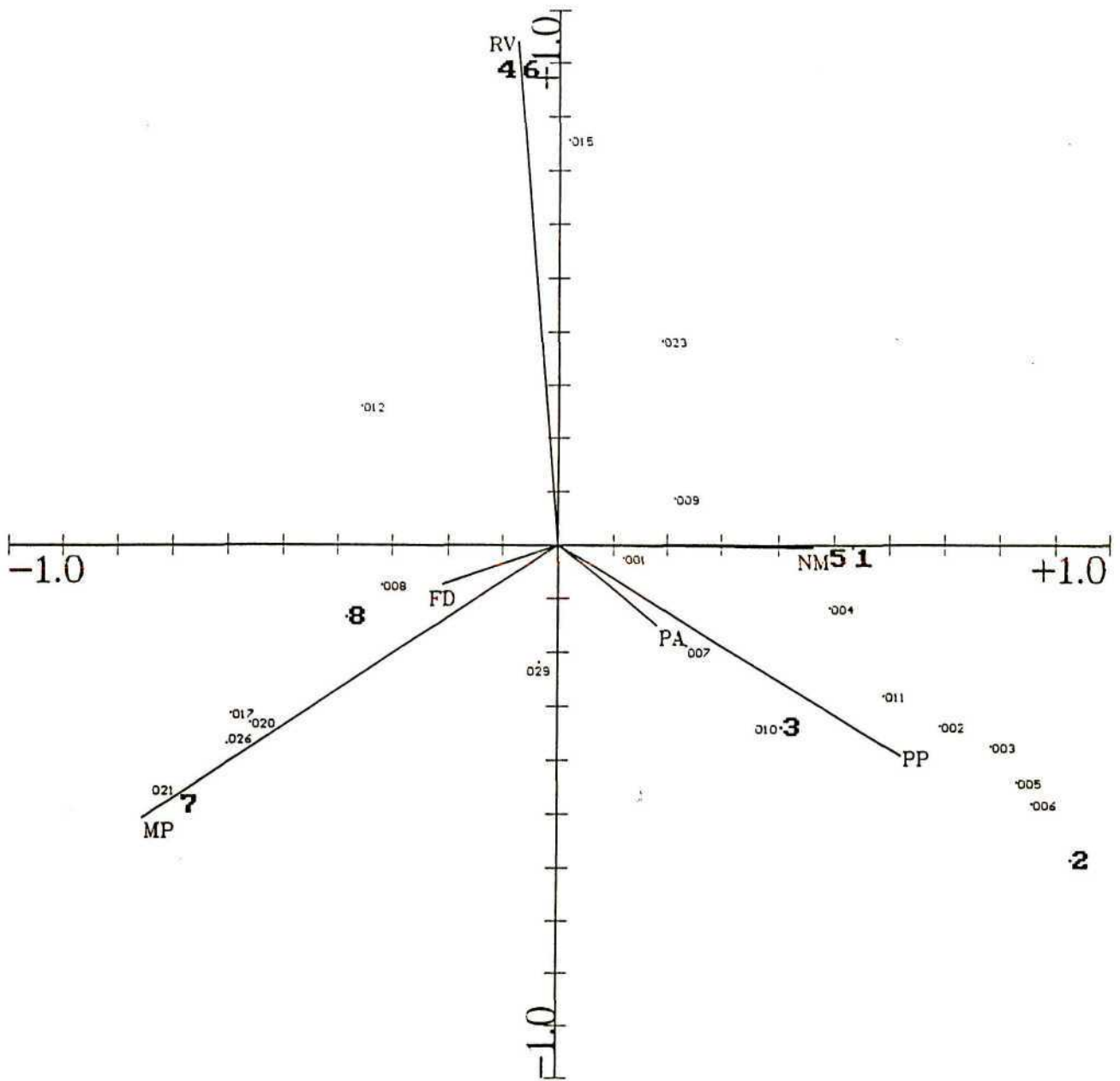


Figure 4.22: Ordination diagram of canonical correspondence analysis (CCA), using data as sum of two sampling seasons (June 1994-May 1996). It is based on environmental variables of management regime 12-17, listed in Section 3.2.4. The diagram shows the distribution of carabid and cicindelid species among the eight sites (1-8 in bold type numbers), and along environmental variable gradients (oblique axis). Species are in small type numbers following the order of listing in Table 4.23. The first axis $\lambda_1=0.641$ is horizontal and the second axis $\lambda_2=0.502$ is vertical.

It is important to note that the ordination diagram in Fig. 4.23 has the same pattern as that of Fig. 4.17 with species data alone. It can be concluded that type of land uses together with soil characteristics can best explain these species patterns.

4.7.2.1.3 CA at the landscape level using species data of the first sampling season

Fig. 4.24 is the CA ordination diagram with species data recorded over the first sampling season. The first axis ($\lambda_1=0.764$) and the second axis ($\lambda_2=0.575$) gave a species % cumulative variance of 48.5%.

The right-hand side of the diagram (Fig. 4.24), (S1, S2 and S3) situated at high altitude are placed closer together just as in Fig.4.17. Species *M. nanum* (140) and *S. fenestratus* (45a) were recorded at S3 only. *Lebiini* sp.(032) was recorded at S1 and S2 but reached maximum abundance in S2. The species *S. alternaris* (254), was recorded at S1 and S3 with maximum abundance in S1.

In the left-hand side of the diagram (Fig. 4.24), S7 and S8 were mapped closer as they shared many species. Specifically species *P. gracilis* (130b) and *C. cylindricus* (40a) were recorded exclusively at S7. The *Harpalini* sp. (150), *Harpalini* sp. (126), *H. tomentosus* (133), reached maximum abundance at S7. The *Harpalini* sp. (115b), although eurytopic to the eight sites, it reached maximum abundance in S7 and S8.

In the top left-hand side of the diagram (Fig. 4.24), the road verge grasslands at S4 and S6, are mapped closer together and therefore are more similar although they were situated at different altitudes. These two grassland sites received the disturbance of burning at the beginning of the sampling season. *D. gilvipes* (250a) was recorded at S4, S6 and S5, but reached maximum abundance at S4. Species exclusive to S4 were, *G. subhamatus* (240a) and *M. atriceps* (181). Site 5 was dissimilar to S4 and S6, as very few species were shared among these sites. The species *H. mnischechi* (105) was exclusively recorded at S5. The *Carabidae* sp. (243) was recorded at S5 and S6 but reached maximum abundance at S5.

Species at the centre of Fig. 4.24, were eurytopic to these sites. Specifically , *C. caffer* (178) was eurytopic to sites in the left-hand side of the diagram (S4, S6, S7). *M. gilvipes* (115a), *H. atratus*

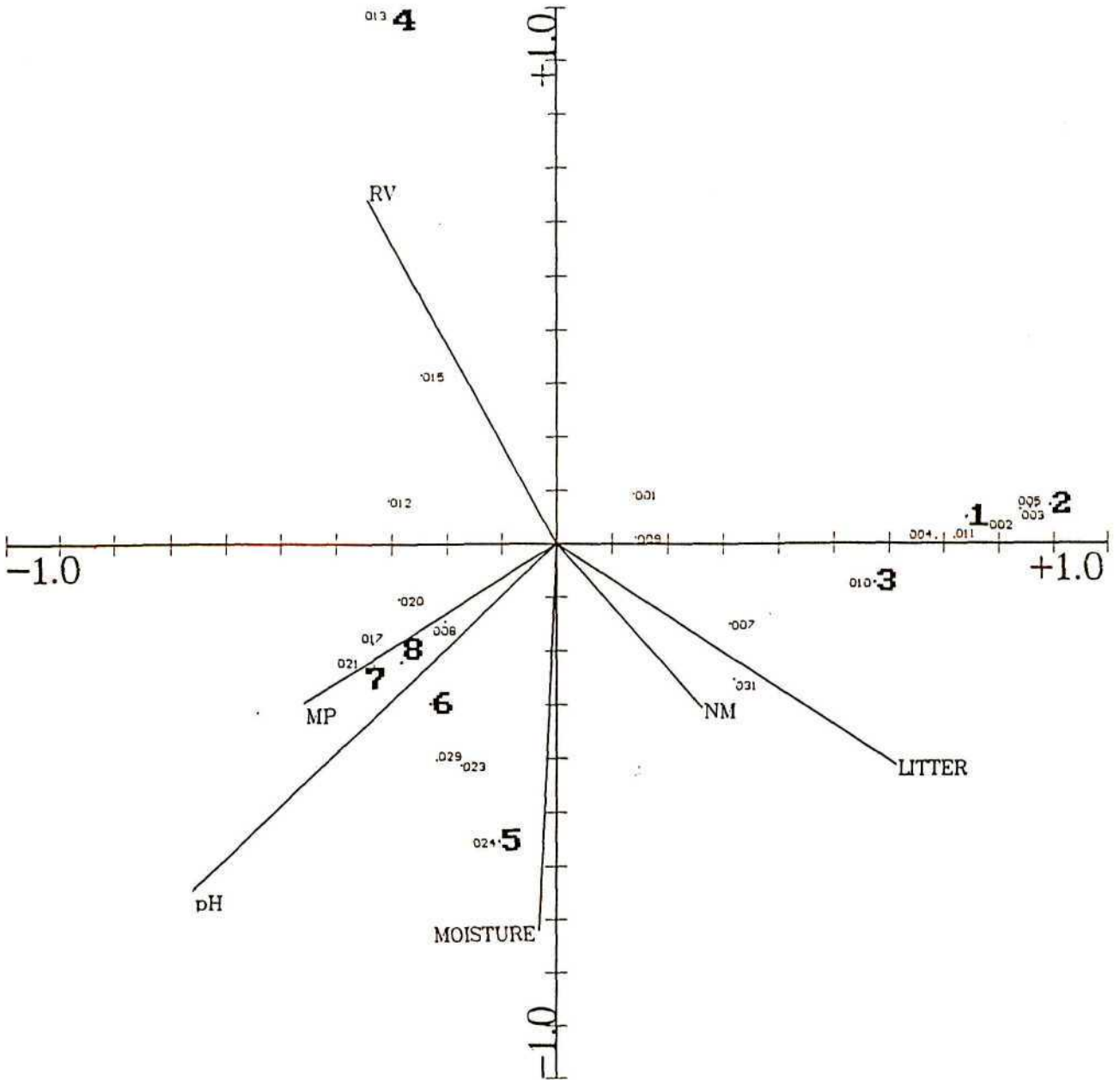


Figure 4.23: Ordination diagram of canonical correspondence analysis (CCA), using data as sum of two sampling seasons (June 1994-May 1996). It is based on environmental variables of soil characteristics 2, 3, 4 and management regime 12, 15, 16, listed in Section 3.2.4. The diagram shows the distribution of carabid and cicindelid species among the eight sites (1-8 in bold type numbers), and along environmental variable gradients (oblique axis). Species are in small type numbers following the order of listing in Table 4.23. The first axis $\lambda_1=0.689$ is horizontal and the second axis $\lambda_2=0.618$ is vertical.

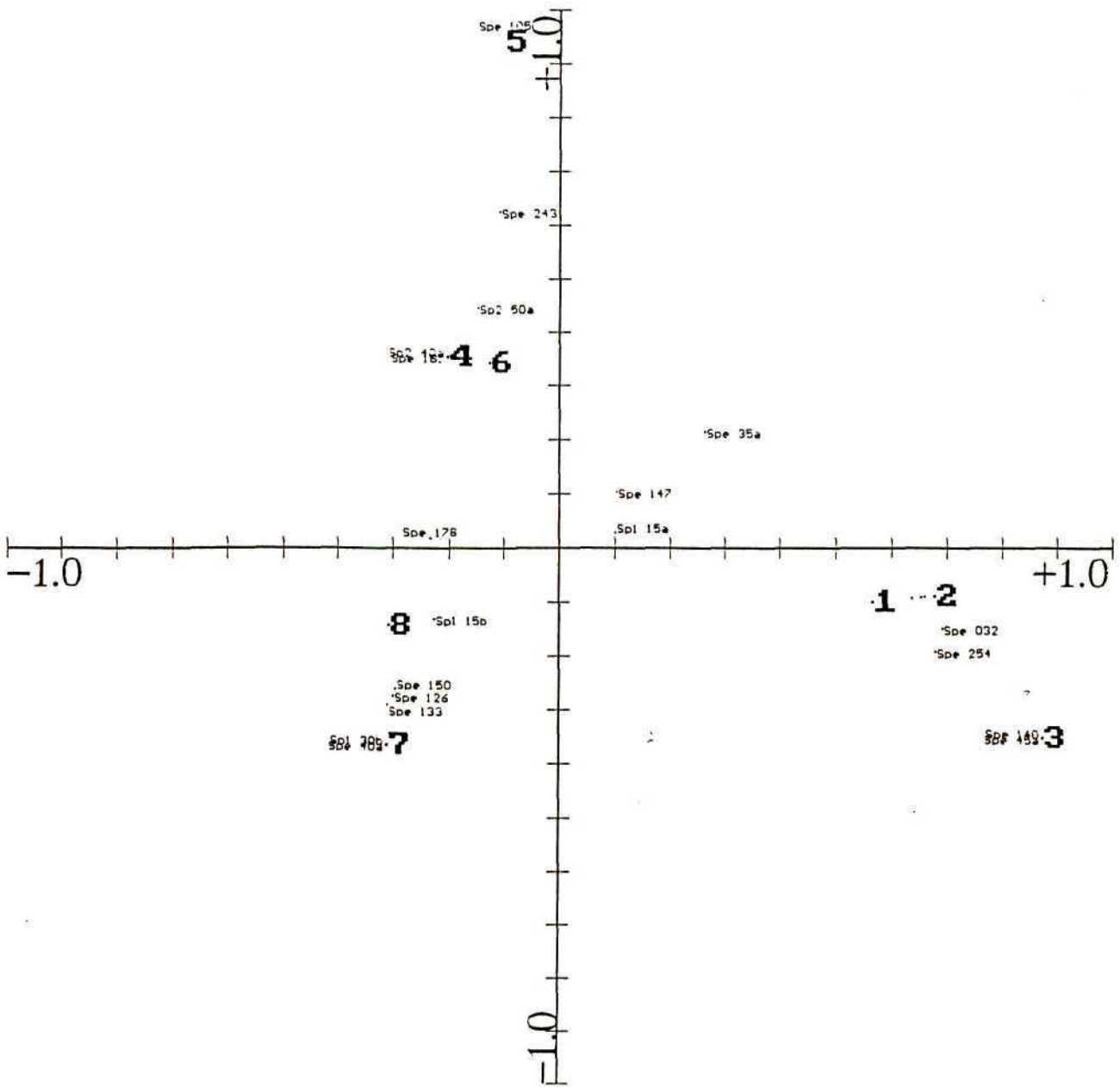


Figure 4.24: Ordination diagram of correspondence analysis (CA), using carabid and cicindelid species data over the first sampling seasons, June 1994-May 1995 (Table 4.21). The first axis $\lambda_1=0.764$ is horizontal and the second axis $\lambda_2=0.575$ is vertical. The diagram shows the distribution of species among the eight sites (1-8 in bold type numbers). Species are shown as code numbers in small type following the order of listing in Table 4.21. CANOCO was used.

(147), and Harpalini sp. (35a) were eurytopic to sites both at high and low altitude.

4.7.2.1.4 CCA at the landscape level using species data of the first sampling season

CCA was carried out with various combinations of the 17 environmental variables as in section 4.7.2.1.2 above. It was found that the combination that best matched the species data was that including variables from soil characteristics namely pH, moisture, twig and litter and from various land-uses being NM, RV and MP (the others were merely reference classes and therefore their omission did not affect the results). Fig. 4.25 displays the ordination diagram with the first axis ($\lambda_1=0.750$) separating sites with high litter from those with high soil pH. The second axis ($\lambda_2=0.571$) separated sites with nature management from those with macadamia plantation and park.

4.7.2.1.5 CA at the landscape level using species data of the second sampling season

The first axis ($\lambda_1=0.737$) and the second axis ($\lambda_2=0.688$) gave a cumulative percentage variance of species data of 48.4%, (Fig. 4.26).

The right-hand side of the diagram (Fig. 4.26), has sites situated at low altitude of the Savanna Zone being S5, S6 and S7. Species *H. mniszechi* (105) and *P. bipustulatus* (256) were exclusively recorded at S5. Carabidae sp. (243) was recorded at S5 and S6 but reached maximum abundance at S5. *L. insidiosa* (130a) was recorded in the nature management sites at S5 and S1.

In the centre of the diagram (Fig. 4.26), are eurytopic species *M. gilvipes* (115a), Harpalini sp. (115b) and Harpalini sp. (35a) that were common to all sites both at high and low altitudes. Species *M. gilvipes* (115a) reached maximum abundance in sites at high altitudes specifically S3 and S4. The Harpalini sp. (115b) reached maximum abundance in sites at lower altitudes at S7 and S8.

In the left-hand side of the diagram, (Fig. 4.26) are sites situated at high altitude being S1, S2, S3 and S4. The sites, S2, S1 and S3 in the top-left hand side of the diagram are more similar in species composition. Specifically, *Abacetus* sp. (213), *C. pseudocastellani* (038) and *Lebiini* sp. (032) were common to S1 and S2. The species *S. alternaris* (254) was exclusively recorded at S1. The species *M. nanum* (140) and *H. atratus* (147) were common to these three sites. *Lebiini* sp. (155) was exclusively recorded at S3.

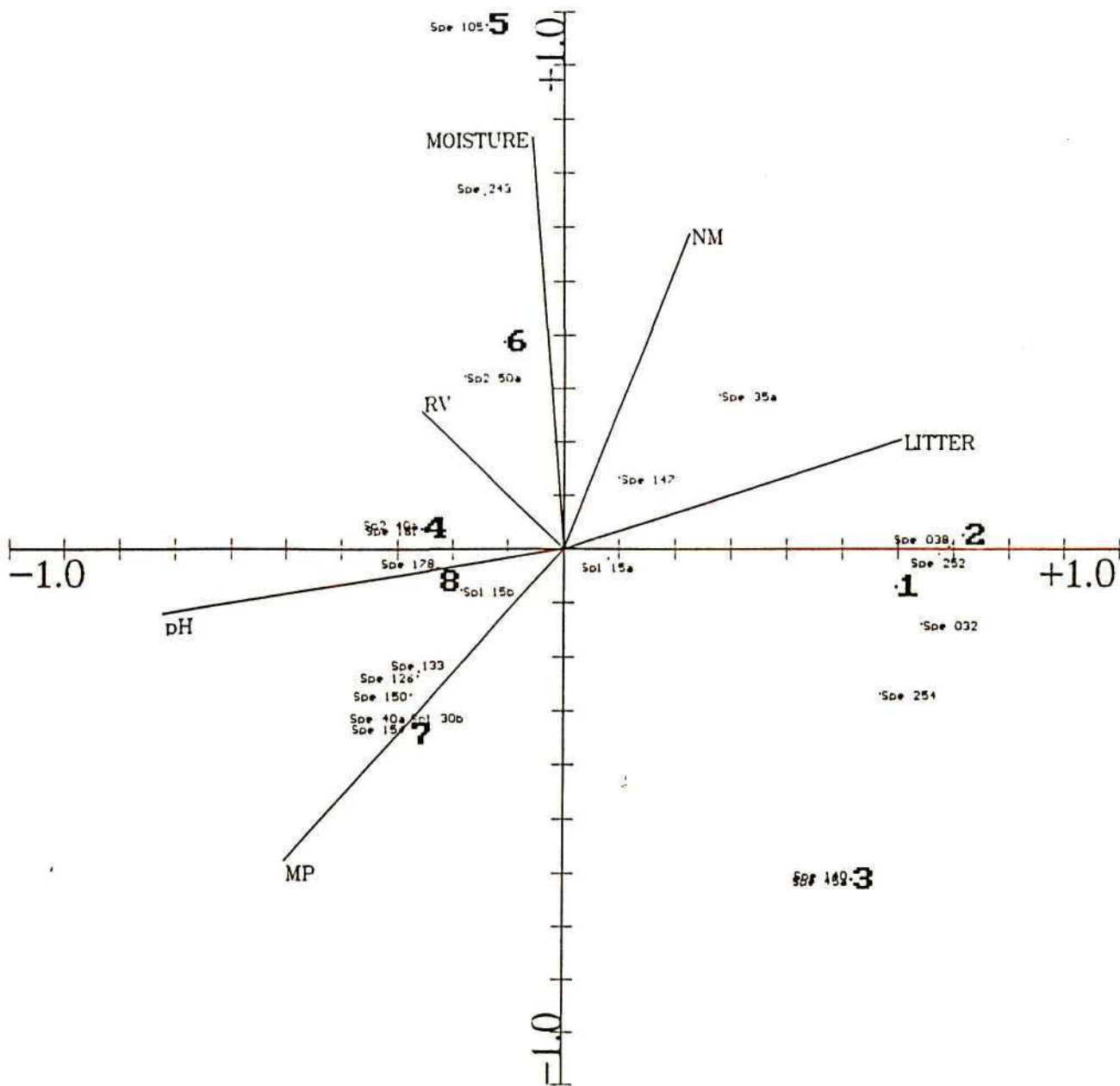


Figure 4.25: Ordination diagram of canonical correspondence analysis (CCA), using carabid and cicindelid species data over the first sampling seasons, June 1994-May 1995 (Table 4.21). It is based on environmental variables of soil characteristics 2, 3, 4 and management regime 12, 15, 16, listed in Section 3.3.4. The diagram shows the distribution of carabid and cicindelid species among the eight sites (1-8 in bold type numbers), and along environmental variable gradients (oblique axis). Species are shown as code numbers in small type following the order of listing in Table 4.21. The first axis $\lambda_1=0.750$ is horizontal and the second axis $\lambda_2=0.571$ is vertical.

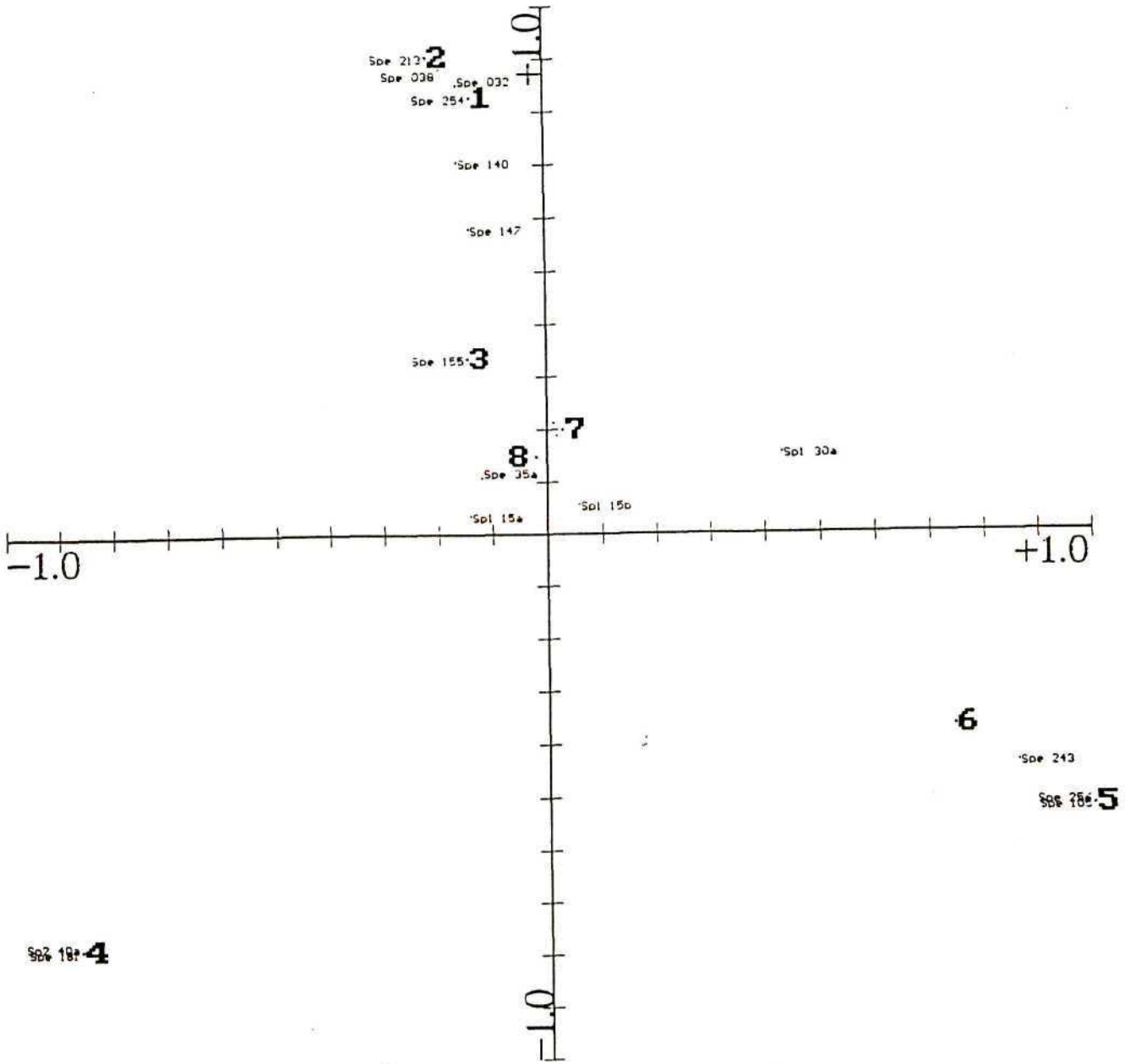


Figure 4.26: Ordination diagram of correspondence analysis (CA), using carabid and cicindelid species data over the second sampling seasons, June 1995-May 1996 (Table 4.22). The first axis $\lambda_1=0.737$ is horizontal and the second axis $\lambda_2=0.688$ is vertical. The diagram shows the distribution of species among the eight sites (1-8 in bold type numbers). Species are shown as code numbers in small type following the order of listing in Table 4.22. CANOCO was used.

In the bottom left-hand side of the diagram (Fig. 4.26), S4 which is a road verge grassland at high altitude was separated from the rest of the sites at high altitude. The species *G. subhamatus* (240a) and *M. atriceps* (181) being the discriminating species. Other discriminating species not shown in the diagram due to space are the cicindelid species *C. inanis*, Cicindelidae sp. (250b) and *D. gilvipes* (250a).

4.7.2.1.6 CCA at the landscape level using species data of the second sampling season

CCA with combinations of 17 environmental variables (section 3.3.4) was carried out. It was found that the combination that best matched the species data was that including variables from soil characteristics namely soil moisture, pH, and litter and land-use variables as NM, RV and MP, (as the other sites were merely reference classes). The ordination diagram is shown in Fig. 4.27. The first axis ($\lambda_1=0.736$) is a moisture gradient and the second axis ($\lambda_2=0.662$) separates sites with nature management and high litter from those of road verges. Details of these results can be seen in Table 4.35. The overall Monte Carlo test statistic was significant ($P=0.03$).

4.7.2.2 Ordination (CA) at the point habitat level

4.7.2.2.1 CA at the point habitat level using species data over two seasons

In the ordination diagram (Fig. 4.28), the eigenvalue of the first axis was ($\lambda_1=0.735$) and the second axis was ($\lambda_2=0.678$) with 32.7% cumulative variance of species data. From the species and point habitats within sites the following can be inferred:

In the right-hand side of the diagram (Fig. 4.28), are point habitat numbers (1-12) belonging to S1, S2 and S3, (Table 4.26 Appendix 2), mapped closer to each other and therefore more similar as they share many species. This pattern was very similar to that at the landscape level, (Fig.4.17). Species recorded in the point habitats (1-12) of these sites were *Lebia* sp. (032), *M. nanum* (011), *S. alternaris* (004), *Lebiini* sp. (002), *C. bonvouloiri* (003), *Abacetus* sp. (006), *S. fenestratus* (010). The most common species were *Lebiini* sp. (002) and *Abacetus* sp. (006). *Lebiini* sp. (002) was recorded in all the point habitats of S1 and S2 and only in point habitat 10 and 12 of S3. It reached maximum abundance in point habitat number 8 of S2. *Abacetus* sp. (006) was recorded in all point habitats at S2 only. The other species were found in some of the point-habitats at the various sites

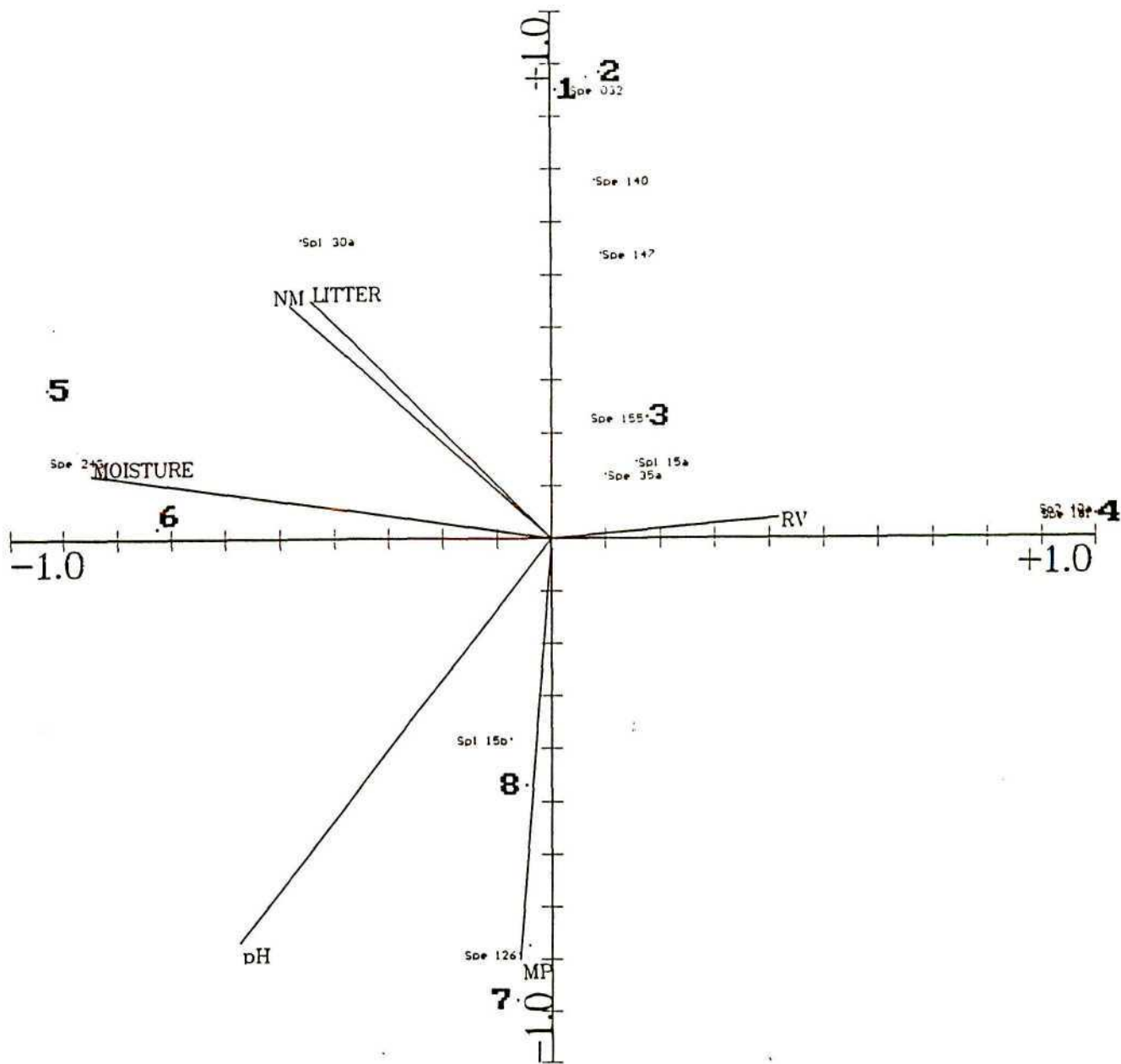


Figure 4.27: Ordination diagram of canonical correspondence analysis (CCA), using carabid and cicindelid species data over the second sampling seasons, June 1995-May 1996 (Table 4.22). It is based on environmental variables of soil characteristics 2, 3, 4 and management regime 12, 15, 16, listed in Section 3.3.4. The diagram shows the distribution of carabid and cicindelid species among the eight sites (1-8 in bold type numbers), and along environmental variable gradients (oblique axis). Species are shown as code numbers in small type following the order of listing in Table 4.22. The first axis $\lambda_1=0.736$ is horizontal and the second axis $\lambda_2=0.662$ is vertical.

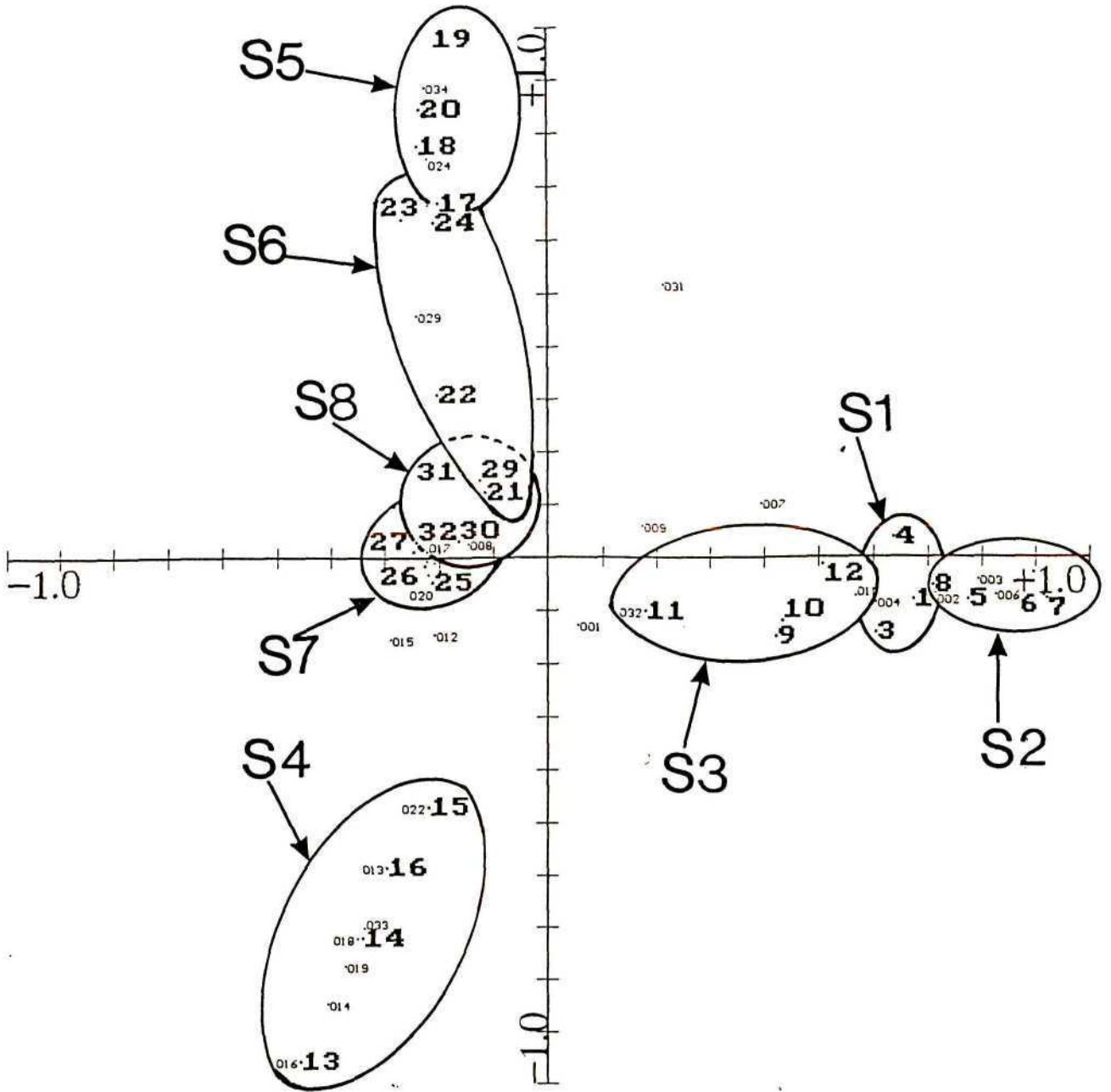


Figure 4.28: Ordination diagram of correspondence analysis (CA) of carabid and cicindelid species data at the point habitat level, using data as sum of two sampling seasons, June 1994-May 1996, (Table 4.26). The first axis $\lambda_1=0.735$ is horizontal and the second axis $\lambda_2=0.678$ is vertical. The diagram shows the distribution of species among the 32 point habitats of the eight sites (S1-S8). Species are shown in small type numbers following the order of listing in Table 4.26. CANOCO was used.

CHAPTER 5

DISCUSSION

5.1 SAMPLING METHODS

5.1.1 Number of species and individuals sampled

A total of 4201 individuals in 35 species were collected by the three trap sampling methods (pitfall traps: $n=4197$; glass window traps: $n=4$ (in two species *Dromica gilvipes* and *Cicindela marginella inanis* which were also collected in pitfall traps); PVC-netting window traps: $n=0$). The visual or hand searching method produced 254 individuals in 19 species, of which 17 species were also caught in the pitfall traps and the other two individuals in two species (*Craspidophorus impictus* and *Chlaenius fasciger*) were caught neither in pitfall traps or in any other trap. The percentage proportions collected by visual searching relative to pitfall trapping in terms of number of individuals was 6% and in terms of species 51%.

Southern African species of Carabidae fall into 30 subfamilies with most occurring in subtropical taxa (Scholtz and Holm, 1986). In total, 250 genera and 1400 species have been recorded from the region (Oberprieler, 1986). However, results of this study show that these numbers are still rising (Table 4.1 with ten undescribed species in Carabidae and one species in Cicindelidae). Carabidae are well-represented in the eastern half of the southern African subcontinent (Oberprieler, 1986) where this study took place. These taxa are: Harpalinae (seven species were sampled here); Lebiinae (nine species were sampled); Chlaeniinae (seven species were sampled) and Pterostichinae (four species were sampled). These four taxa comprised 73% of the total 33 species of Carabidae collected. The other 27% was made up of fauna more peculiar to the western half of the southern African subcontinent.

The western part of southern Africa harbours a fauna more peculiar to southern Africa, with numerous less subtropical taxa. Examples are, the Axinidiini species *Metaxinidium nanum*, which is rare, (Scholtz and Holm, 1986) and was recorded in very low abundance in the mistbelt

indigenous forest, adjacent pine plantation and park grassland, all of which were at a high elevation (900 m). Also, the apterous Graphipterinae and Anthiinae (not recorded in this study) are particularly abundant in southern Africa (Oberprieler, 1986). The Graphipterinae species *Graphipterus cordiger subhamatus* was recorded in a road verge grassland, where it preferred open sandy areas from autumn burning.

All four cicindelid species were found in the high elevation-sandy road verge grassland. Only one of these species, *Dromica gilvipes*, was recorded at another road verge at lower elevation after a fire disturbance. To date, about 30 genera and 150 species of Cicindelidae have been recorded from the region (Oberprieler, 1986). A great majority of the southern African Cicindelidae belong to the tribe Cicindelini (Scholtz and Holm, 1986), particularly to the genus *Dromica*, of which two species were recorded here, and the genus *Lophyra* (of which no species were recorded here). Also, one species in the genus *Cicindela*, and one undescribed Cicindelidae species, were also recorded.

The last comprehensive work on the southern African Carabidae was by Peringuey (1896). Major groups that have been studied since then are Harpalinae (Basilewsky, 1950); Reicheiina (Basilewsky, 1980); Pterostichinae (Straneo, 1958) and the genus *Graphipterus* (Basilewsky, 1977). For the family Cicindelidae, the last comprehensive work was by Horn (1926). Since then, Rivalier (1971) has introduced major changes to the classification of the African fauna. The latest studies of the southern African Cicindelidae are those of Basilewsky (1966) and Cassola (1975a,b).

In the macroecological context, patterns in carabid assemblages in forest and grassland habitats in the northern hemisphere are moderately species rich (Lovei and Sunderland, 1996). Usually, about 10-40 species can be active in a habitat in the same season. Regional assemblages are correspondingly richer (Horvatovich and Szarukan, 1986; Luff, 1987; Thiele, 1977; Van Dijk, 1987). Generalizations are difficult, as the extension of an assemblage in space or time is usually not defined. The total number of species also depends on the method and intensity of sampling and on the type of habitat sampled (Spence and Niemela, 1994) (see also Table 5.1). Currently, more powerful data-handling has made it possible for continental and regional distribution patterns to be described and evaluated (Luff *et al.*, 1989; Eyre and Luff, 1990a; Turin and Essen, 1990; Comandini and Taglianti, 1990; Luff *et al.*, 1992; Niemela and Spence, 1994;

Penev and Turin, 1994; Rykken *et al.*, 1996; Dufrene and Legendre, 1997). The numbers of species and individuals caught in forest and grassland habitats in this study can be said to be species rich assemblages. This is strongly supported by the lognormal distribution patterns illustrated in Fig. 4.6a,b and Fig. 4.8.

There is a taxonomic impediment with regard to the southern African species, particularly Harpalinae. In addition, there is no correspondence between the species recorded from the northern hemisphere (references above) and those in this study (Table 4.1). However, the general patterns of species richness and abundances in different habitats between northern and southern hemisphere is generally similar.

This is the first study in southern Africa to characterize habitats according to their carabid and cicindelid assemblages. There is a large gap in the number of species collected in this study to those already recorded (Oberprieler, 1986) and still awaiting taxonomic verification (in the National Museums, personal communication from Dr Endrody Younga, Transvaal Museum and Dr. Tanza Clark, Durban Museum).

It has been shown that carabids have a major role to play in environmental research (Stork, 1990; Niemela, 1996a). However, there is a glaring deficiency in our knowledge of these animals in the southern hemisphere, which can only be addressed by increasing ecological research and the training of more taxonomists (Lawton *et al.*, 1998). Although macroecological trends in other parts of the world can be modelled and applied to local patterns (Brown, 1995; Blackburn and Gaston, 1998; Niemela *et al.*, in press), endemic and rare species usually require specific conditions (Niemela *et al.*, 1987).

5.1.2 Collecting methods

The main sampling method was pitfall trapping, supplemented by glass window traps, PVC-netting window traps and visual (hand) searching.

5.1.2.1 Pitfall trapping

Pitfall trapping was found to be the most economic, simple and efficient sampling method for carabids and cicindelids here in South Africa.

Although the relative merits of pitfall trapping compared to other methods is continuously debated, it still remains the best method for most studies of carabid distribution and relative abundance (Spence and Niemela, 1994; Digweed *et al.*, 1995; Dufrene and Legendre, 1997) (see also Table 5.1). Despite criticisms of pitfall trapping, the method has contributed enormously to making carabids popular 'model organisms' in conservation and land use evaluation (Lindroth, 1992; Desender *et al.*, 1994; Luff, 1996; Dufrene and Legendre, 1997). For instance, most of the studies presented at the 3rd International Symposium of Carabidology were based on pitfall trapping, and about 75% of them dealt with questions related to the effects of human activities on carabids in conservation studies (Niemela, 1996a, b). This southern hemisphere study corroborates these northern hemisphere studies.

5.1.2.2 Glass window traps

Glass window traps appear to have the potential for trapping beetles in more open and in frequently-disturbed habitats such as sandy road verge grasslands. These habitats are likely to be colonised by species that fly (Den Boer, 1970, 1990). Cicindelid species (*Dromica gilvipes*, *Cicindela marginella inanis* and *D. tuberculata carinulata*) caught in these traps, flew in short bursts when disturbed. The forest habitats sampled were fairly stable with minimum anthropogenic disturbance, which may be one reason for the absence of carabids in the window traps. This suggests that the majority of carabids in these forest habitats do not or rarely fly. Studies in the northern hemisphere have shown that the proportion of flightless individuals in dimorphic species increases with increasing habitat persistency and time since colonization (Den Boer *et al.*, 1980). The proportion of macropterous *Pterostichus melanarius* can be as low as 2% in stable habitats e.g. old forest patches (Den Boer, 1970) or as high as 24-45% in less stable ones e.g. newly reclaimed polders of Netherlands (Haeck, 1971).

5.1.2.3 PVC-netting window traps

PVC-netting window traps here did not provide a good barrier into which flying carabids and cicindelids could bump and slide into the collecting trough. Indeed, no carabids and cicindelids were caught after six months using this method. Although these traps were very conspicuous and were frequently disturbed by humans and wild animals, glass provided a better barrier. Overall, pitfall trapping was found to be the most selective method for collecting carabids for

landscape evaluation in South Africa.

5.1.2.4 Visual searching

Results of visual searching (Section 4.1.2) clearly showed that more species and individuals were caught by pitfall trapping than by visual searching at all of the eight sites. Species were more active in the morning than in the afternoon, possibly because higher afternoon ground temperatures inhibited activity. Preiszener and Karsai (1990) studied the diel activity patterns of carabid beetles on a sandy grassland in eastern Europe and found that soil temperature and light intensity seem to be the most important factors in regulating of activity of carabids on sandy grassland. Although there are many factors that influence the efficiency of visual searching, e.g. individual sampling effort, the reason for not seeing and catching many carabid species may be that there are more nocturnal than diurnal species. For instance, *Pachydinodes bipustulatus* was observed during visual searches resting under logs during the day. The same species has been seen (personal observation) flying around domestic lights at night. The use of automatic time-sorting mechanisms has been applied in field studies and has provided detailed data on diel activity patterns of carabid beetles in field situations (Desender *et al.*, 1984; Luff, 1978; Alderweireldt and Desender, 1990). In the UK, 60% of all known Carabidae species are nocturnal and 20% diurnal (Luff, 1978). The diurnal activity dendrogram for carabids in UK woodlands revealed groupings for diurnal, nocturnal, and crepuscular species, plus species that overlap in some of these categories (Dennison and Hodkinson, 1984). Changes in temperature (Jones, 1979), light intensity and humidity (Thiele, 1977) also influence activity.

An additional two species were caught by visual searching over and above pitfall trapping. These two species occurred on grass stems rather than on the ground, which is probably the reason for their absence in pitfall traps.

All the four Cicindelid species recorded in this study were seen within the first 30 minutes of a visual search in the road verge grassland. This indicates that tiger beetles can be used easily in environmental monitoring and assessment because of the high probability of being seen and sampled (Dufrene and Legendre, 1997; McGeoch and Chown, 1998). Pearson and Cassola (1992) have reported that at a site in Peru, it took only 50 hours of observation to find 93% of the tiger beetle fauna, and to find 90% of the butterfly species entailed nearly 1000 hours of field

work, yet the butterfly list of over 1200 species is still rising. Pearson and Cassola (1992), proposed the use of tiger beetles (Cicindelidae) as a good indicator group for identifying areas for biodiversity conservation. Indeed, the road verge grassland had the highest diversity in all the eight sites. In addition, this study has shown that cicindelids may be good indicators even though only four species were recorded in this study. These few species indicated certain conditions, namely a good fire management regime.

Tiger beetles are well known, their biology well understood, they occur over a broad range of habitat types and geographical areas, and they also exist in remnant patches of appropriate habitats (Pearson, 1988; Pearson and Cassola, 1992). Clark and Samways (1997) also found that cicindelids were particularly useful as fast indicators of certain habitat types relative to disturbance. The importance of scale must be emphasized (May, 1993). Choice of scale influences the choice of indicator taxon or taxa. Whereas cicindelids were much more sensitive indicators at a micro scale (1 m x 1 m) (Clark and Samways, 1997), butterflies were good indicators of habitat type and landscape pattern at the meso scale (50 m x 50 m) (Wood and Samways, 1991) in the same area.

Although visual searching is more labour intensive than pitfall trapping, it appears that it can give reliable qualitative estimates of species compositions. The percentage proportions collected by visual searching relative to pitfall trapping in terms of number of individuals was 6% and in terms of species 51%.

Niemela *et al.*, (1988) supplemented pitfall trapping with hand picking, sieving and sweep-netting in coniferous forest. By hand-picking and sieving, 54 individuals from 10 species were collected with a sampling effort of 350 working-hours. No carabids were found in the sweep-netting samples. Pitfall traps collected 1986 individuals from 42 species. Samples from sieving and hand-picking did not include a single species that was not caught using pitfall traps. Whereas hand-picking and sieving appear to be labour intensive, resulting in poor catches in forest landscapes, Eversham and Telfer (1994) found that direct searching provided a more qualitative sample, which was more reliable than pitfall trapping in sandy road verges. This method appears to be well suited to the fauna of sparse vegetation on light soils (Eversham and Telfer, 1994) as it involved hand sifting of the top 4-5 cm of sand in random areas of 1 m². This study supports these findings, as can be seen from results of visual searching in road verges, but

recognises the need to supplement visual (hand) sampling with pitfall trapping in open habitats that are not necessarily sandy.

Spence and Niemela, (1994) compared three methods of sampling carabid beetles: litter-washing technique, extraction by Tullgren funnels and pitfall trapping. They found that large-bodied species predominated in pitfall samples and small-bodied species predominated in litter samples. They also found that uncovered, round pitfall traps yielded generally higher catches than rectangular or covered, round traps, but that the pattern was not consistent over all species or over all five forest habitats sampled. However, patterns of seasonal occurrence of carabids were similar in data from different trap types. From these comparisons, Spence and Niemela (1994) concluded that ecological studies of carabid populations and assemblages using pitfall traps may be improved if they are both designed and interpreted in light of the biology of the group and with regard to the deficiencies of pitfall trapping.

The use of unfenced pitfall traps is advisable in intensive, long-term studies on the population dynamics of epigeal arthropods and in determining their relative abundances (Spence and Niemela, 1994; Sunderland *et al.*, 1995) in forest and grassland habitats, Mommertz *et al.* (1996) suggested that in arable habitats, fenced pitfall traps should be used at least in addition to unfenced traps. Mommertz *et al.* (1996) showed that, in sampling of epigeal arthropods in agro-ecosystems, short-term D-Vac suction sampling was not appropriate for Carabidae, Staphylinidae or Lycosidae because relatively large and heavy individuals were underestimated. Unfenced pitfall traps were found to overestimate the percentage of Carabidae present but underestimate the Staphylinidae. The dominance structure of the Carabidae assemblages at the sampling sites was more similar for the two trapping methods.

Many studies have not reported the use of light traps in sampling carabid beetles. A personal observation of the species *Pachydinodes bipustulatus* and *Microcosmodes laetusculus* at domestic lights at night suggest the need for light traps to supplement pitfall trapping so that one can maximise catches of nocturnal flying species. Indeed, some species in the group Scaritinae are attracted to light in large numbers (Oberprieler, 1986). This trap should be a design incorporating a glass window and a light source.

Sampling methods in these studies support the conclusions of Spence and Niemela (1994);

Luff (1996) that it is indeed important to tailor a sampling programme to the species and habitats with which one works and interpret the data obtained from a sound base of biological intuition. The choice of a sampling method depends on the questions being asked. In surveys of large geographical areas where the objective is qualitative inventory and comparison of assemblages, pitfall trapping is the only realistic alternative presently available (Van den Berghe, 1992; Niemela *et al.*, 1990, 1993; Niemela, 1996b; Sunderland *et al.*, 1995; Dufrene and Legendre, 1997).

5.1.2.5 *Linking collecting methods to data analyses*

All the analyses in this study have been carried out using pitfall trapping data resulting in meaningful conclusions. Luff *et al.* (1989) classified and ordinated 248 habitats of ground beetles in north-east England. Most of the data used for classification and ordination consisted of records from the database of the national ground beetle recording scheme-UK. Each record consisted of simply a presence/absence list of species recorded from a locality, irrespective of the methods of collecting used, size of locality or time span over which the list had been made. This analysis was based on a large data set (3062 records, 152 species and 248 sites), but also a very imperfect one. There was no standardization of collecting effort or technique, and the species list varied from five or more species recorded on a casual visit to one spot, to comprehensive lists of up to 100 species collected from a wider locality over several years. Despite such 'noisy data', the analyses led to an interpretable classification and ordination of carabid communities, which was also the case in studies of Eyre and Luff (1990).

Currently, there is a strong need for information about the state of natural ecosystems, especially for invertebrates (Samways, 1994; Niemela, 1997; Lawton *et al.*, 1998). This study has shown that pitfall sampling carried out during one year, or at least the whole activity season of the species, gives a reliable estimate of the densities of active adult individuals (Baars, 1979; see others in Table 5.1) or is a good predictor of mean biomass and of the species quantitative importance (Loreau, 1992). The dominance scale obtained from pitfall sampling is far from the real dominance scale in the wild (Halsall and Wratten, 1988; Niemela and Spence, 1994). Therefore, there are potential problems in interpreting the equitability or diversity of species assemblages. However, it has been shown that multivariate analysis of data from sampling programmes that have been conducted under standardized conditions can lead to meaningful

results (Luff *et al.*, 1992; Dufrene and Legendre, 1997). Niemela *et al.* (in prep.) have proposed a global programme that uses a common methodology (pitfall trapping) in the same taxonomic group (carabid beetles) in visually similar land-mosaics but in different parts of the world. Carabids are taxonomically and ecologically abundant and sensitive to environmental changes to be a reliable signal of human-caused disturbances (Dufrene and Legendre, 1997).

5.1.3 Collecting preservative

Some of the preservatives used in trapping carabids include ethylene glycol, formalin, detergent and water, or salt solutions, or no preservatives at all (Table 5.1). There appears to be no obvious correlation between numbers and or species caught and preservative used. However, this has yet to be proved scientifically. The choice of preservative appears to depend more on intervals between emptying periods (Van den Berghe, 1992; Holopainen, 1990) and the cost. In this study, ethylene glycol kept specimens fresh for intervals up to 30 days in the field. Ethylene glycol (ethanediol), known as antifreeze, has been used for long intervals especially in the northern hemisphere (Morill, 1975; Van den Berghe, 1992; Bedford and Usher, 1994; Kajak and Lukasiewicz, 1994; Niemela *et al.*, 1993; Eversham and Telfer, 1994). It is also used as an antifreeze coolant for motor-vehicle engines and is therefore easily available in petrol service stations even in the developing world. However, it is considered carcinogenic and is not available in all countries (e.g. Canada).

In this study, formalin was abandoned because of its high toxicity and the extra caution it requires when transporting and handling it in the field. Although the use of a saturated salt solution was tried (as salt is very cheap and easily available), it was not suitable in the hot savanna areas as it dried out completely during hot days.

Holopainen (1990) found that ethylene glycol had a stronger attractive effect on carabid beetles than on other soil surface-active arthropods such as Staphylinidae, Collembola, Acari and Araneida. He noted that, although the use of ethylene glycol as a preservative increases the trapping efficiency of pitfall traps, it may lead to biased estimates of species composition and female/male ratio of carabid communities. He also showed that the use of water and a 1% salt solution and detergent was adequate as preservative for as long as a week. In feeding studies involving visual examination of carabid gut contents of aphid remains, plain water (without

preservative) is required (Scheller, 1994).

5.2 SPECIES CUMULATIVE CURVES

During sampling from winter (June) to autumn (May), the species cumulative curves (Fig. 4.1a,b,c) reached an asymptote by the 10th sampling replicate (March), end of summer in almost all habitats. Most species were collected over the spring and summer months of September to March. Further species after these months, from autumn through winter (i.e. April to August), were rare and contributed little to the general trends (Table 4.29).

Studies in the northern hemisphere have shown that adult longevity can exceed one season. Many species from the tribes Agonini, Harpalini, Pterostichini, Carabini have life spans longer than one year (Thiele, 1977). Individuals from field populations of several species from different parts of the world, e.g. Europe (Gergely and Lovei, 1987; Houston, 1981; Luff, 1982; Van Dijk, 1972; Wallin, 1988); Japan (Sota, 1984) and the Sub-Antarctic (Davies, 1987), can live for up to four years and reproduce more than once. Generally, long adult life-span is more common in large species and in species with winter larvae (called autumn breeders) than in ones with summer larvae or spring breeders (Lovei and Sunderland, 1996).

From a macroecological context, results of species cumulative curves over the two annual sampling seasons and the presence of many large species (6 mm - 25 mm see Table 4.36) appear to suggest that these species are characterized by relatively long adult life-span, which may enable them to be used in short-term carabid sampling (spring sampling, summer sampling, autumn sampling) for site assessment studies. Carabid beetles have the potential for use as ecological indicators in nature conservation research (Stork, 1990). For example, the evaluation of the ecological value of different sites within the framework of environmental planning or in the assessment of the changes that take place on a site subjected to nature conservation management (Luff, 1987). Unfortunately, limitations in resources usually reduce the possibility of large-scale research effort, and in particular, the length of the sampling (Maelfait and Desender, 1990; Lawton *et al.*, 1998). Maelfait and Desender (1990) found that carabid beetle faunas did show differences between comparable sites using data sets from short periods: spring, summer and autumn pitfall sampling. However, they warned that such studies are best interpreted by specialists of the animals concerned.

Spring sampling of carabids was employed by Rykken *et al.* (1997) in a study of ground beetles as indicators of land type diversity in the green mountains of Vermont. Three ecological land types (each ranging from tens to hundreds of hectares) were sampled. Traps were kept open for 30 consecutive days over spring and many spring breeding carabids (9041 individuals in 35 species) were captured. Analysis of data, especially by ordination (DECORANA) led to interpretable results (see further details in section 5.7.1.3).

5.3 SEASONAL POPULATION VARIATION

Comparison of seasonal population variation between forests and grasslands at the same altitude, different altitudes, primary and secondary forests has shown that, although disturbance increases beetle populations in all habitats, very intensive disturbance decreases populations. Thus, the intermediate disturbance hypothesis (Connell, 1978; Huston, 1979) is also supported here (see section 5.4 for details).

5.3.1 Effect of altitude

Carabids from the two geographical Zones here, Savanna (700 m.a.s.l.) and the Escarpment (900 m.a.s.l.) had two peaks of activity during each annual season. The first and highest peak was in early summer, and the second, smaller peak was in late summer. These activity peaks were positively correlated with rainfall, temperature and humidity (Tables 4.1.1 and 4.1.2 and Fig. 4.2 a,d). These Zones lie within the summer rainfall region of southern Africa. It will be interesting in the future to compare the activity patterns of these animals with those in areas within southern Africa that receive winter rainfall e.g. the Cape region.

In Italy, Comandini and Taglianti (1990) have shown that carabid communities of coastal zones (120-740 m.a.s.l with Evergreen and Oak wood vegetation) in Mediterranean areas appear to have two peaks of activity, a first, lower peak in spring and a second, higher peak in autumn. Summer is a dry period in the Mediterranean areas, and activity of carabids on the soil surface is reduced due to the negative water balance of soil (Comandini and Taglianti, 1990). The opposite situation occurred in mountains (520-1300 m.a.s.l with Beech wood vegetation), without a dry period but with high rainfall (1000 mm), where there was only one peak of carabid activity in summer which shifted towards end of summer in the lowest and warmest Beech woods.

The altitudinal difference of about 200 metres between the Escarpment and Savanna Zones in this study did not have an effect on peak beetle activity. But it did influence total climate in terms of total rainfall, temperature, humidity and vegetation type which, in turn, determined species assemblage composition (see also section 5.5). In a Belgian, zoogeographical study, environmental factors such as climate (e.g. rainfall, temperature, number of days with frost) and edaphic features (lithology, pedology, geology) were shown to be closely related to altitude. There were only small differences between these maps (i.e. climate and edaphic factors) and those of ecological districts established by biogeographers (Dufrene, 1990). When distribution patterns obtained from ecological factors were compared with those obtained from carabid beetles, the maps showed that carabid distribution patterns were less clear than those of ecological factors, and that carabid distribution was often related to habitat type. Among ecological factors, edaphic factors played a more important role in carabid distribution than did macroclimate. This was also shown to be the case for another insect group Apoidea-Hymenoptera (Dufrene, 1990). The importance of soil characteristics (section 5.7.1.1) relative to climate and human-defined habitats in determining beetle distributions is also supported here. Therefore, this study and those of Dufrene (1990) and Rykken *et al.* (1997) have shown that, Hengeveld's (1985) proposition on the role of climatic factors in carabid distribution and the implied existence of biogeographical provinces appears not to be the case. Dufrene (1990) and Rykken *et al.* (1997) have pointed out that the interpretation of biogeographical classifications is much more intricate than some authors have suggested (Bailey *et al.*, 1978; Rowe and Sheard, 1981; Spies and Barnes, 1985; Hengeveld, 1985; Avers *et al.*, 1993). See further details of discussion in section 5.7.1.3.

5.3.2 Activity patterns

Carabids from the two geographical Zones here, Savanna (700 m.a.s.l.) and the Escarpment (900 m.a.s.l.) had two peaks of activity during each annual season. The first and highest peak was in early summer, and the second, smaller peak was in late summer.

The population troughs in this study were in June-July (winter) and December-January (mid-summer) (Fig. 4.2a, d). The mid-summer reduction in beetle activity may be because either the species became dormant or because heavy rains inhibited their activity, or that there is prevalence of species with two generations in one season.

Seasonal rhythms with dormant periods during winter and/or summer are an integral part of the life history of temperate-region ground beetles (Lovei and Sunderland, 1996). Generally, the activity of most beetles peaks in either spring or autumn. These activity peaks usually coincide with the reproductive period (Goulet, 1974; Carter, 1980; Loreau, 1985) although the connection between activity and reproductive rhythms is flexible in many species (Makarov, 1994). Results of seasonal population patterns in this study and those of Niemela *et al.* (1992); Goulet (1974) and Barlow (1970) suggest that adults that emerge from pupation later in the summer overwinter, sometimes after a small peak of activity in the late summer or early autumn.

Outside tropical regions, the cues regulating these cycles involve temperature and photoperiod (Thiele, 1977). Seasonal activity and reproductive rhythms in tropical species are regulated by seasonal changes in soil moisture and flooding (Paarman, 1986).

For decades, carabid species, at least in the northern hemisphere, have been divided into spring and autumn breeders. Recently, Den Boer and Den Boer-Daanje (1990) ranked 68 most common carabid species of Drenthe (The Netherlands) according to the period of reproduction, and they found a continuous sequence from early spring to late autumn, including (1) some species that mainly reproduce in winter, (2) some species that show two reproduction periods in the same year, and, (3) species that uninterruptedly reproduce during the greater part of the year. The adults of most species hibernate after reproduction and again participate in reproduction in following years. This suggests that a division in adult and larval hibernators is inadequate. These features were found to be common to carabids of western Europe. Den Boer and Den Boer-Daanje (1990) have therefore suggested rejecting the traditional concepts of spring-reproducing vs autumn-reproducing species, and adult overwinterers vs larval overwinterers, in favour of categories containing species with summer larvae vs winter larvae or species with vs without diapausing larvae (Hurka, 1986).

5.3.3 Effect of disturbance

The seasonal population variation in these landscapes appear to be at least partly habitat-specific and are affected by the intensity and type of disturbance, seasonal climatic changes from one year to the next and adjacent habitats which influences the number of individuals at a given site. In the relatively less disturbed landscapes (forests), species composition and dominance structure

of the carabid fauna over the two years studied, were relatively constant. For instance, the natural indigenous forest and pine plantation (about 200 m apart) shared many species. Nevertheless, the abundances of these species varied considerably. Tree pruning in the pine plantation had the effect of increasing overall abundance at this site, although the composition of species remained similar across the two sampling seasons at both sites. The species assemblages in the macadamia plantation and a natural *Acacia*-woodland were different, apparently due to quite different vegetation types and structures. There was little seasonal population variation within each site. However, the overall proportionate abundance in the natural *Acacia*-woodland (9.20 %) was much less than that in the macadamia plantation (49.44 %) where the degree of disturbance was higher.

In grassland landscapes, species assemblages on the intensively managed mown lawn of the park varied greatly from one season to the next. Many species were rare and were recorded in one season but not the next. Species turnover was high, hence the total number of species recorded at this site was high. This park is an area surrounded by a pine plantation and natural indigenous forest. Some of these species could have been vagrants from the surrounding areas, although others clearly lived under stones and in leaf litter.

Species compositions in road verge grassland habitats at different elevations were only similar when the nature of management (fire) was applied to both sites in one season and different in the following annual season when fire management was applied to one of the sites. The autumn fire disturbance at the high altitude road verge grassland, initially lowered numbers, but as soon as the grasses began to flush in spring (after three months), the numbers increased greatly. Cicindelids dominated at first and then carabids in the absence of fire the following season. Alternating fire management across seasons appears to provide habitats for different assemblages of species. This has important conservation management ramifications which are discussed in Chapter 6.

The composition of species (and not the dominance structure) in the low-altitude hayfield were more similar to those of the adjacent macadamia plantation than to those of the low altitude road verge grassland. In addition, autumn burning in grassland resulted in a higher abundance, while autumn mowing in the hayfield resulted in a lower abundance.

Overall, the park (with intensive lawn management) had the highest seasonal population variation due to the absence of shelter and food. In contrast, the natural indigenous forest had the least population variation.

It is well known that spatial and temporal variation in insect assemblages on different scales masks the clear interpretation of observed patterns in species abundance and distribution (Samways, 1993). The season of sampling may affect the catches, because some species occur early in the season and some later (Niemela, 1996b). In addition, there is variation between years, which requires long-term monitoring. In some cases, variation from one year to the next in the same assemblage may be greater than variation in the same year between neighbouring assemblages. For instance, Sanderson (1994) reports that within a farm-level experiment, 47% of the variation in invertebrate assemblages was explained by between year differences and 17% by within-year environmental variation.

In late successional habitats, such as mature forests, populations tend to be more stable than in early successional stages and in disturbed habitats, such as cultivated areas (Loreau, 1992, 1994). Furthermore, only a few carabid species tend to dominate numerically in late successional habitats, suggesting that variation in community parameters is primarily driven by these abundant species (Niemela, 1993a). An especially stable habitat for carabids appears to be the mature boreal forest, as assemblages in geographically distant areas have similar species compositions and are dominated by the same species (Niemela *et al.*, 1988; Niemela *et al.*, 1993; Niemela *et al.*, 1994b). However, these studies also indicate that wide temporal variation is common in carabid assemblages, and that this may mask and confound spatial effects. Niemela (1996b) warns that it is wise to cautiously interpret results from studies involving spatial and temporal heterogeneity. Moreover, sampling covering only one field season obviously cannot provide more than a snapshot view of the dynamics of a carabid assemblage, and subsequent snapshots of the same assemblage would probably show different patterns (Niemela *et al.*, 1986a).

In addition to abiotic environmental variables, species interactions may affect carabid occurrence. There is some evidence that interspecific competition may affect the structure of carabid assemblages and even cause character displacement (Niemela, 1993b). Also, most competition studies have focussed on adult beetles, but competition among larvae or between larvae and

adults maybe more important (Lovei and Sunderland, 1996). Carabid occurrence appears to be determined by a multitude of biotic and abiotic factors acting together (Niemela 1996b). The relative importance of these factors may vary from species to species (Loreau, 1992). Numerically dominant species may be affected by interspecific competition, and less abundant species may be primarily influenced by abiotic conditions. Moreover, the relative importance of these effects may vary from year to year; for instance in one year, biotic effects may be more important and the following year, abiotic conditions may be the determining factor.

The use of carabid communities as indicators of environmental quality and change depends on their being a sensitive and consistent reflection of their environment. This study and those of Luff (1990); Gruttke and Weigmann (1990); Maelfait and Desender (1990); Dufrene (1990) support this statement.

For instance, Luff (1990) sampled carabid beetles by pitfall trapping for eight years in a mosaic of grass and arable plots. Differences between the catches from each habitat were attributed to habitat preferences of each species rather than from true population differences. The rankings of the commoner species were similar in each year, but there was occasional high catches of particular species. Also some species appeared to show extinctions and refoundings, as suggested by Den Boer (1977). The data also showed a gradual decline in species richness over the years. This was attributed to a change in the surrounding habitats.

Temporal variability is particularly important in insect conservation biology because insect populations fluctuate so much (Samways, 1990). The suggestions from the results of variability measures is that any species can become extinct no matter how abundant it is, should conditions go against its continued survival (Samways, 1990, 1996; Lockwood and De Brey, 1990). Indeed, the Rocky Mountain grasshopper, which, in the middle of the last century was so common and a serious pest in western USA, was extinct by 1902.

5.3.4 Population phenology: multivariate analysis (PCA) of species abundances over time

Dufrene *et al.* (1990) used correspondence analysis (CA) to compare the temporal distribution of carabid communities in two different regions in Belgium. The same technique has been employed here, using PCA instead of CA, and has shown that PCA gives a better visual impression of the actual species abundance relative to each other and to the sampling period

(month) using the species oblique axis. It is also a quick and easy way of comparing activity patterns such as timing of occurrence and abundance of individual species in many habitats. For instance, in the ordination diagrams (Fig. 4.3c-k), *Metagonum gilvipes* (115a) was very abundant in the natural indigenous forest (Fig. 4.3c); adjacent pine plantation (Fig. 4.3d) and macadamia plantation (Fig. 4.3i) in late spring to early summer (September-9 to November-11), while in the Savanna *Acacia* woodland (Fig. 4.3g) and road verge grassland (Fig. 4.3f), this species was most abundant in late summer (February-2 to April-4).

From these ordination diagrams (Fig. 4.3c-k), it is also easy to see that the activity patterns in each of the eight sites (Fig. 4.3c-j) and in the whole study area (Fig. 4.3k) (i.e. the two geographical Zones) are very similar. The succession of sampling periods (months) almost forms a ring in the ordination diagrams. This suggests that the first and the last sampling periods (months) in an annual season are more similar because the same species were caught in winter (June-6 to July-7) and again the following year in late autumn (April-4 to May-5). This means that there is some degree of activity taking place throughout the year. For instance, there are some species whose activity is highest in autumn, especially in road verge grasslands (Fig. 4.3h,j) e.g. the undescribed Harpalini species 115b and 35a and others with winter activity (Fig. 4.3k). Winter activity was mainly in grassland habitats because they are relatively warmer than forests. Erwin (1979) and Niemela *et al.* (1992) found that the warmer and more open grasslands in recently-cut sites in boreal forest provided a more favourable habitat for carabids. Overall, carabid species richness was higher in these habitats than in the boreal forest.

From these ordination diagrams, it is also easy to see and compare the activity patterns such as timing of occurrence and abundance of individual species over time (months). For instance, e.g. *M. gilvipes* (115a), were most abundant in early summer (October-10 to November-11) and late summer (February-2 to March-3), with dormant periods in mid-summer (December-12 and/or January-1) and in winter (June-6 to July-7). This study therefore recommends the use of PCA instead of CA in such studies.

5.4 SPECIES DIVERSITY AND THE INTERMEDIATE DISTURBANCE HYPOTHESIS

Trends in the response of species to various landscape disturbances reported in other studies (Mossakowski *et al.*, 1990; Kegel, 1990; Niemela *et al.*, 1993; Lawton *et al.*, 1998) were similar

to those found in this study. In grasslands, anthropogenic disturbance increased species richness more so by fire than by cutting. However, intensive disturbance results in sink habitats (e.g. park). In forests, disturbance appeared to decrease species richness but increase abundances. The most species-rich habitats were those with intermediate disturbance (Huston, 1979).

Diversity results require to be interpreted with caution. Increasing levels of environmental stress have generally been considered to decrease diversity (e.g. H'), decrease species richness (e.g. Margalef's $R1$) and decrease evenness (e.g. Pielou's J'), i.e. increase dominance (Connell, 1978; Huston, 1979). However, this interpretation may be an over-simplification of the situation. More recent theories on the influence of disturbance or stress on diversity suggest that in situations where disturbance is minimal, species diversity is reduced because of competitive exclusion between species; with a slightly increased level or frequency of disturbance, competition is relaxed, resulting in an increased diversity, and then at still higher or more frequent levels of disturbance species start to become eliminated by stress, so that diversity falls again. Thus, it is at intermediate levels of disturbance that diversity is highest (Connell, 1978; Huston, 1979). Therefore, depending on the starting point of the community in relation to existing environmental stress levels, increasing levels of stress (e.g. induced by pollution or anthropogenic disturbances) may result in an increase or decrease in diversity. It is difficult, if not impossible, to say at what point on this continuum the community under investigation exists, or what value of diversity one might expect at that site, if the community were not subjected to any anthropogenic stress. Thus, changes in diversity can only be assessed by comparisons between sites along a spatial gradient or with historical data (Huston, 1979).

5.4.1 Potential problems of diversity indices

In this study, measures of species richness and diversity showed that there are potential problems in interpreting the equitability or diversity of species assemblages (He *et al.*, 1994; Dufrene and Legendre, 1997). Following illustrates this point:

Shannon's diversity index H'

Shannon's diversity index H' showed that grasslands and forests at higher elevation (900 m.a.s.l.) with an Escarpment climate and high annual rainfall (1100 mm) had higher diversity than the grassland and forest sites at lower elevation (700 m.a.s.l.) with a savanna climate and low annual

rainfall (700 mm). This appears to suggest that climate and altitude are playing a role. When altitude is kept constant (900 m.a.s.l.), grasslands with fire and cutting disturbance (road verge and park) had higher diversity than did indigenous forest with nature management or a pine plantation. Thus, the northern hemisphere observations that forests do not support as diverse carabid fauna as do open, human-modified habitats (Thiele, 1977; Spence, 1990; Niemela *et al.*, 1992b) are also supported here. Within grasslands at high elevation, a road verge with fire disturbance had higher diversity than a park with cutting disturbance. Within forests, the indigenous forest with nature management had higher diversity than pine plantation in the middle successional stage with forestry management. At the lower elevation (700 m.a.s.l.), the same pattern was observed in grasslands where a road verge with fire disturbance had higher diversity than a hayfield with cutting disturbance. However, the macadamia plantation with agricultural disturbance had a higher diversity (resulting from intensive irrigation) than did the natural *Acacia*-woodland.

Margalef's species richness index (R1) and the rarefaction model

Measures of species richness using the Margalef's species richness index (R1) and the rarefaction model were only similar when data from two seasons were combined. Interpreting results using these indices from one season can be highly misleading. Therefore, it appears that it is important to collect data from at least two seasons if sound conclusions are to be made when comparing different habitats using these indices. Comparing species richness of these habitats using pooled data showed that the overall picture was similar to that of Shannon's diversity index H' . Grasslands and forests at higher elevation (900 m.a.s.l.) had higher species richness than those sites at lower elevation (700 m.a.s.l.). This suggests that climate and altitude were playing a role. When altitude was kept constant (900 m.a.s.l.), grasslands with mowing and fire (park and road verge) had higher species richness than natural indigenous forest or pine plantation. Within grasslands, a mowed park had higher species richness than a burnt road verge (contrary to Shannon's diversity H'). The indigenous forest had higher species richness than the managed pine plantation in a middle successional stage (similar to Shannon's diversity H'). At lower elevation (700 m.a.s.l.), a burnt road verge grassland had higher species richness than a mown hayfield (similar to Shannon's diversity H'). *Acacia*-woodland had higher species richness than the macadamia plantation (contrary to Shannon's diversity H').

These species richness indices showed that the recreational park grassland overall had the highest species richness out of all the grassland and forest sites both at high and low altitude. However, this site had the lowest abundance and the highest species turnover of all sites, which casts doubts on interpreting the results of the species richness indices.

Theoretical number of species (S^*) from the lognormal model

Ludwig and Reynolds (1988) have recommended the use of the rarefaction model or theoretical number of species (S^*) from the lognormal model to compare species richness between different habitats. Therefore, the theoretical number of species (S^*) from the lognormal model was applied.

Using the theoretical number of species (S^*), the overall effect of climate and altitude in separating landscapes appeared to disappear. Keeping altitude constant (900 m.a.s.l.), species richness was highest in the burnt road verge (similar to Shannon's diversity H' and contrary to R1 and Rarefaction indices) and lowest in the intensively mown park grassland (contrary to R1 and Rarefaction indices). The burnt road verge grassland had the greatest species richness and the park had the lowest species richness (similar to Shannon's diversity H' and contrary to R1 and Rarefaction indices). In turn, the indigenous forest had greater species richness than the pine plantation (similar in all the indices). At 700 m.a.s.l., species richness was greatest in a macadamia plantation (contrary to all the diversity indices) and lowest in the mown hayfield (similar for all the indices). The macadamia plantation had a greater species richness than the *Acacia*-woodland (similar to Shannon's diversity H' and contrary to R1 and Rarefaction indices).

Contrary to Shannon's diversity H' and R1 and Rarefaction indices, the (S^*) model showed that the macadamia plantation had the greatest species richness. From pitfall trap data and visual observations at each of these sites, it was expected that macadamia plantation would have the highest species richness, because this is where the majority of the species collected appeared to be reproducing. Whereas at the park, most species were recorded in extremely low abundance with high turnover i.e. many species were present one season but absent the next. These species were vagrants from adjacent habitats or they were not able to survive in the park. This suggests that the (S^*) model for comparing species richness in different habitats appears to be the most

appropriate one.

According to the S* model, the macadamia plantation was the richest in carabid species, followed by the natural, moist indigenous mistbelt forest. The pine plantation in the an intermediate successional stage was the least species rich. Grassland sites, with autumn burning, were the richest in carabid species.

These results indicate caution in interpreting results of species richness of different habitats, especially using the rarefaction model and Margalef's index (R1). These indices showed for instance, that the park was rich in carabids species, when in fact it is a sink habitat.

There is a need for the identification of characteristic or indicator species in nature monitoring, conservation, and management (Dufrene and Legendre, 1997). The most commonly-used criteria for assessing the conservation value of a site is species richness, but richness is sensitive to several factors. He *et al.* (1994) has shown how some of the commonly used indices of diversity vary in a nonlinear fashion with the size of the elementary sampling unit (quadrats etc.) as well as with the extent of the study area. Also, high diversity does not ensure that a site has a high ecological value (Dunn, 1994). Dufrene and Legendre (1997) have noted that even where the sampling effort has been equal across sites, species diversity is a questionable criterion when habitats with different productivity are compared, or when the number of rare species is large. Moreover, the protection of high-diversity sites does not guarantee the effective conservation of rare or spatially restricted organisms (Prendergast *et al.* 1993). Therefore, as proposed by Webb (1989), representativeness, or representative diversity, would be a more satisfactory criterion. This implies a typical species assemblages for habitats or ecological factor combinations.

According to Thiele (1977), pitfall trapping is the best technique available for assessing species assemblages at any one site. Pitfall sampling carried out during one year, or at least the whole activity season of the species, gives a reliable estimate of the densities of active adult individuals (Baars, 1979) or is a good predictor of mean biomass and of the species quantitative importance (Loreau, 1992). The dominance scale obtained from pitfall sampling, however, is far from the real dominance scale in the wild (Halsall and Wratten, 1988; Niemela and Spence, 1994). Therefore, there are potential problems in interpreting the equitability or diversity of species assemblages. However, it has been shown that multivariate analysis of data from sampling

programmes that have been conducted under standardized conditions can lead to meaningful results (Luff *et al.*, 1992; Dufrene and Legendre, 1997). In this study, the use of multivariate statistics, interpreted the data more clearly. For instance, with species diversity indices, it was not clear what factors were important in determining species patterns. On the other hand, with multivariate analysis these factors were clearly defined.

Studies in the northern hemisphere appear to show similar responses by carabid beetles to anthropogenic disturbance. Kegel (1990) studied the distribution of carabid beetles in the urban area of west Berlin. He studied street margins with various intensities of disturbance ranging from ruderal habitats with no management, through poorly-managed habitats (no irrigation and two mowings), intensively managed habitats (irrigation, several mowings, fertilizers and pesticides) to park-like stands. He found that ruderal habitats with no management and poorly managed habitats had higher numbers of species than intensively-managed habitats. He found that the number of species was correlated more with the level of management and the size of individual areas of study than to the location within or outside of the urban centre. A cluster analysis clearly separated domestic gardens and park-like stands from open habitats. Gardens and parks were characterized by a low number of individuals and a relatively high number of species. Xerophilous species preferring open landscapes dominated the street margins, whereas the gardens showed a greater proportion of species which prefer forest habitats. Repeated mowing and intensive irrigation leads to drastic changes of abiotic conditions which prevent seed-production of the plants, thus seed-feeding carabid species will be eliminated and forest dwelling species will increase (Kegel, 1990). Similarly, in this study here the park habitat with intensive mowing had a species composition similar to that of adjacent forest habitats (Kegel, 1990).

Mossakowski *et al.* (1990) studied carabid beetles as indicators of habitat destruction caused by military tanks in northern Germany. They found the number of species increased along the gradient of destruction because of the increase in the diversity of habitat structure. In particular, species preferring sandy soils appeared in open sand patches. Only at sites with a higher degree of destruction did number of species approach towards zero. On the other hand, number of individuals fitted expectations better, and decreased along the gradient of destruction. Mossakowski *et al.* (1990) also found that the number of species and individuals that are able

to fly increased along the disturbance gradient.

Niemela and Halme (1992) showed that carabid species diversity and richness in fields and pastures were the most diverse, and forests the least diverse of Åland Island in SW Finland. The low diversity of forest carabid assemblages as compared with cultivated areas has also been demonstrated in a study from the mainland Finland (Niemela *et al.*, 1987). The results suggest that forests do not support a high diversity of adult carabids. Only a set of very few species seem to be able to maintain high population numbers in forests. Whether this is caused by unsuitability of the environment for adults or larvae remains unanswered (Spence, 1979).

5.4.2 Caswell's neutral model and estimating environmental stress levels

Caswell's neutral model estimates environmental stress levels. Here it showed that diversity in the *Acacia*-woodland was significantly below neutral model predictions ($V=-2.14$), and the diversity at all other sites was close to neutrality. This suggests that the carabid community was under some kind of environmental stress in the *Acacia*-woodland. Indeed, this site had the lowest evenness with one undescribed Carabidae sp. (243) making up 77% of the total (Fig. 4.5). It is possible that this species is an exotic or that it has recently colonized this habitat. However, deviations in diversity H' from the neutral model prediction depends only on differences in evenness, since the species richness is fixed and the evenness component in diversity may behave differently from the species richness component in response to stress. Therefore, it is quite possible that the intermediate disturbance hypothesis (Connell, 1978; Huston, 1979) had a bearing on the behaviour of V in response to disturbance. Increased disturbance may cause it either to decrease or increase, as can be seen in Table 4.30. Confirmation of this result can only be achieved if changes in diversity at this site can be assessed by comparisons with historical data (which are currently absent) or by increasing the sampling effort over a wide range of habitats to obtain additional annual data. The biology and taxonomy of this dominant species would also have to be determined. This model has been applied to aquatic systems (Clarke and Warwick, 1994).

Bisley nature reserve where part of this study took place is hot and dry, with a mean annual rainfall of 705.5 mm. The vegetation can be divided into four distinct habitat types: Low Open Woodland, Low Closed Woodland, Short Riverine Thicket and Wetland (Hurt, 1987). The

riverine thicket is the habitat type that was studied here, and consisted of almost 100% woodland. The Riverine Thicket occurs on deep soils along the water courses and is characterized by a dense, impenetrable structure dominated by *Acacia karroo* (Hayne), *A. ataxacantha* (DC.), *Rhus* sp. and *Buddleja saligna* (Willd.). Having determined the carabid species within this Riverine Thicket, further research is required to determine the carabid species of the other three distinct Savanna vegetation types within Bisley nature reserve. The Low Open Woodland and Low Closed Woodland are found on shallower soils away from the watercourses. The Low Closed Woodland is severely infested with exotic *Lantana camara*, as well as mature specimens of *A. sieberana* (usually an open woodland species), *A. nilotica* and *A. karroo* (both of which are predominantly closed woodland species). This suggests that infrequent burns and the encroachment of *L. camara* have resulted in a change from open woodland to closed woodland in parts of the reserve (Hurt, 1986).

The undescribed Carabidae sp. (243) and, *Hystrichopus mniszechi* together made up 88% of the total catch. The other species were rare, but with high species turnover over the two seasons. Three species recorded in the first season were absent in the second season. Similarly, five new species were recorded in the second season that were absent from the first. Autumn burns spilling over from adjacent road verges are likely to be partly responsible for this high turnover, particularly as the single dominant species was common to these two sites.

Species unique to this savanna Riverine Thicket woodland were *H. mniszechi*, *Lebia immaculata* and an undescribed Harpalini sp. (35b), the latter of which was common in the sandy wet shores of an intermittent river. This *Acacia* woodland and the indigenous high-elevation forest both supported the species *Lebia nematopeza insidiosa*, suggesting that it is characteristic of natural forest irrespective of altitude and type.

5.5 EFFECT OF DISTURBANCE ON BODY SIZE

Carabids currently recorded in southern Africa are small to large (3 mm -60 mm) and cicindelids are medium-sized to large (10mm - 70 mm) (Oberprieler, 1986). Species recorded in this study ranged from 4 mm to 30 mm in length. The mean body size of carabid assemblages in forests and grasslands decrease both with increasing intensity of disturbance. Grasslands with little cutting (a field of hay mown once a year) had the highest mean body size (16.83 mm) and

autumn burnt grasslands had the lowest mean body size (10.38 mm and 11.17 mm). The tree dominated *Acacia*-woodland had the highest mean body size (13.40 mm) and the macadamia plantation had the lowest (11.31 mm).

These findings support those for carabids in the northern hemisphere. The mean body size of carabid assemblages in woodlands, moors and grasslands in northeastern England was related to several environmental factors (Blake *et al.*, 1994). The higher the intensity of disturbance the more large species were lost from the assemblage. Species body-size distribution within carabid assemblages was similarly displaced toward smaller values as urbanization increased (Sustek, 1987). In Berlin, urban habitats are inhabited by smaller carabid species (Klausnitzer, 1989; Kegel, 1990), and is directly related to intensity of disturbance. Lovei and Sarospataki (1990) compared carabid beetles in agricultural fields in Eastern Europe to assemblages from Western Europe. Assemblages in Eastern Europe were, on average, more species rich than those in Western Europe. Although the mean size of the common species did not differ between Eastern and Western Europe, there were more larger (>10 mm) species in the East.

5.6 GRAPHICAL DISTRIBUTION PATTERNS: SPECIES-ABUNDANCE RELATIONSHIPS

The lognormal model and x2 geometric curves (Figs. 4.6a,b and 4.7a,b) showed that disturbed forests (pine and macadamia plantations) had fewer rare species yet more common ones. Natural forests (high-elevation indigenous forest and *Acacia*-woodland) on the other hand, had more rare species. Burnt grassland had more rare species than common ones, while mown grassland had few rare species and very few common ones. The infrequently mown grassland (hayfield) had more common species than the frequently mown one. Disturbed grasslands had higher numbers of rare species than all forests. Pine plantation had many common species and the least number of rare species. The same pattern of higher numbers of rare species in grasslands as compared with forests has been documented in the northern hemisphere (Niemela *et al.*, 1987; Niemela and Halme, 1992; Niemela *et al.*, 1992b).

All the eight sites showed lognormal distribution curves. The lognormal curves (Fig. 4.6a,b and Fig. 4.8) suggest that all the sites have heterogeneous assembly of species, with most of them, having intermediate abundances, and only a few being being very abundant or rare. It may also

be that these relative abundances are a product of the interplay between many independent factors (Ludwig and Reynolds, 1988). The effect of some of these factors particularly, environmental ones, have been analysed using multivariate methods.

5.6.1 x2 geometric plots

The purpose of graphical/distributional representations is to extract information on patterns of relative species abundances without reducing that information to a single summary statistic such as a diversity index (Clarke and Warwick, 1994). Unlike multivariate methods, these distributions may extract universal features of community structure which are not a function of the specific taxa present, and may therefore be related to levels of biological stress. For instance, Gray and Pearson (1982) suggest that it is the species in the intermediate abundance classes 3 - 5 that are the most sensitive to pollution-induced changes and might best illustrate the differences between polluted and unpolluted sites (i.e. this is a way of selecting 'indicator species' objectively). Clarke and Warwick (1994) have applied this method to aquatic systems successfully.

In this study, comparisons of the structural features of the graphs in Fig. 4.7ab, across two seasons, showed a clear drop in class 3-5 abundance classes during the first season after fire in the road verge grasslands (S4 and S6). Species falling in these abundance classes are the indicator species of these sites. At S4, such species are *Metagonum gilvipes*, *Dromica tuberculata carinulata*, *Cicindela marginella inanis*, *Dromica gilvipes*, *Graphipterus cordiger subhamatus* and undescribed Harpalini species (150, 35a and 115b). The other sites did not show any obvious structural differences across the two sampling seasons due to lack of any major disturbance. It is expected that species in these geometric classes (3-5) would be the most sensitive to disturbances at these sites. These results show that this method can be applied to terrestrial monitoring for effects of disturbance.

In monitoring programmes designed to evaluate the impact of management practices, it is useful to weight the species abundances at a site to account more for the typical than the vagrant species (Dufrene and Legendre, 1997). In addition, Dufrene *et al.* (1990) and Dufrene and Legendre (1997) have showed that carabid beetles have considerable potential as bioindicators. They suggest that, a good bioindicator must always be collected when its habitat is sampled and that

the best bioindicator carabid beetles are those which are present in all the sampling stations of one habitat type (Dufrene *et al.*, 1990). Therefore, this study supports those of Gray and Pearson (1982), Clarke and Warwick (1994) and Dufrene and Legendre (1997) and also values carabids as bioindicators.

Carabids are good bioindicators of aquatic as well as terrestrial systems (Casale, 1990). Like other aquatic or semi-aquatic insects, most hygrophilous carabid beetles can be excellent indicators of the ecological conditions of marshes and rivers. Carabids were used to monitor the deterioration of aquatic ecosystems resulting from pollution by herbicides, fertilizers, poor water management and drainage in Italy. Ecosystems sampled included (1) banks and riparian woods along rivers; (2) shores of lakes or peat-bogs (3) periodically flooded woodlands (4) small pools on rocky or peaty soil (5) large rice fields. A total of 143 species were collected. Although this number of species was not high compared to the total number of species recorded in Italy (1300 species), it was rather high when compared to the whole carabid fauna of some north European countries e.g. 350 species in the UK (Casale, 1990). In this study, although aquatic ecosystems were not sampled, the undescribed Harpalini species 35b, was collected from the sandy wet shores where it aggregated, this is an indication that there are carabid beetles of aquatic and semi-aquatic habitats in the southern hemisphere which can be employed in bioindication studies (Dufrene and Legendre, 1997) and also for identifying areas of high conservation value, as has been shown by Casale (1990) in Italy. Casale (1990) found that, the majority of species in these habitats were fully winged, as already made evident by authors for other unstable ecosystems (Brandmayr, 1983). Therefore, these environments are important 'reservoirs' for carabids with high dispersal power (Den Boer, 1970). In these habitats, some rare or very rare species were found. A qualitative comparison of these biotopes revealed a high degree of faunal dissimilarity. Each locality had at least one exclusive species. Therefore, there is a need to create and conserve heterogenous areas, as species with low dispersal powers are particularly threatened due to effects of habitat isolation (Den Boer, 1970; Turin and Den Boer, 1988; Desender and Turin 1989).

Lawton *et al.* (1998) have warned that, no one group serves as a good indicator taxon for changes in the species richness of other groups. This, suggests the need to understand the ecology of all taxa for better informed decisions in the planning of biodiversity conservation. Studies of the

biodiversity of several animal groups (birds, butterflies, flying beetles, canopy beetles, canopy ants, leaf-litter ants, termites and soil nematodes) along a disturbance gradient (near-primary, through old-growth secondary and plantation forests to complete clearance) in tropical forest in Africa led to these conclusions (Lawton *et al.*,1998). Species richness generally declined with increasing disturbance. The proportion of morphospecies and the number of scientific hours required to process samples both increase dramatically for smaller bodied-taxa. Data from these eight groups indicated the huge scale of the biological effort required to provide inventories of tropical diversity, and to measure the impacts of tropical forest modification and clearance. Even though this is an impediment that may not be solved in the near future, it has been shown in this study that, carabid beetles have a current big role in ecological and environmental studies.

5.6.2 Lognormal distribution model

Other graphical/distributional representations, to extract information on patterns of relative species abundances without reducing that information to a single summary statistic such as a diversity index, were employed by Niemela (1993a) for solving the mystery of the ‘missing species’ in species-abundance distributions of boreal ground beetles where the lognormal distribution model was employed.

A recurring pattern in community samples is that a few species are abundant, while the great majority are scarce (Preston, 1962; Hughes, 1986; Ludwig and Reynolds, 1988). Many mathematical models have been developed for these species-abundance distributions, but the biological interpretation of the models is often contradictory (Magurran, 1988). Consequently, Gray (1987) suggested a study of community organization by comparing species-abundance distributions. Niemela (1993a) used this approach to demonstrate a peculiarity in the structure of carabid assemblages in boreal forest, where carabid species-abundances often resemble the log series model with the mode in the first octave, and the dominant species are distinctly separated from the scarce ones (Niemela *et al.*, 1987b, 1990). In other words, there is a ‘gap’ between the abundant and scarce species. According to the commonly held view, as sample size increases with time or space, the log series grades into the log normal (Magurran, 1988). Niemela (1993a) found this not to be the case in the species-abundance distributions for carabid samples from the boreal forest, as increasing sample size did not close this ‘gap’ in mature forest, thinned forest and recently-cut forest. However, in the intermediate age classes (2-20

years since cutting) such a 'gap' was not present. This 'gap' in assemblages was not only detected in boreal forest in Finland but also in Belgian forests (Loreau, 1992) and in some mature forest types in boreal North America (Niemela *et al.*, 1992b, 1994a). The absence of this 'gap' in the intermediate age classes (2-20 years since cutting) was attributed to the increase in species of open habitats and a decrease in species of forest habitats (Niemela, 1993a). The warmer and more open grasslands in recently cut sites provide a more favourable habitat for carabids. Overall carabid species richness is higher in these habitats than in boreal forest (Erwin, 1979; Niemela *et al.*, 1992b). Thus, it appears that a few species have adapted to the boreal forest to be able to maintain high population numbers (Loreau, 1992). These observations have been explained by the availability of food (Hengeveld, 1980) and interference by *Formica* ants (Niemela *et al.*, 1992a). Loreau (1992) has proposed that the dominant species are regulated by competition and that scarcer species are regulated more by the physical environment.

In carabid samples from the eight sites in this study, species-abundance distributions appeared to give similar patterns to those found in boreal forest (Niemela, 1993a). For instance, in the autumn-burnt road verge grasslands and, park grassland, there was no 'gap' in the octaves separating dominant species from scarce ones. Although in the annually-mown hayfield, this 'gap' was present in alternating octave numbers (3, 5 and 7).

This gap was present in all forest habitats here. In natural indigenous forest (over 150 years) and an adjacent pine plantation (12 year-middle successional stage), the gap was present in octave number 5 (with 16 -32 individuals). The similarity between these two forests may be the result of sampling carabids as far as 40 m from the edge in the natural indigenous forest and interior species may have been missed. Alternatively, it may have been because this remnant indigenous forest patch had undergone relaxation to lower species richness.

In the *Acacia*-woodland, the gap between dominant and scarce species was present in octave numbers 6 and 7 (with 32-64 and 64-128 individuals). Carabid sampling in this site was between 10 m and 500 m apart. There was only one dominant species in octave number 8 (256-512 individuals), this was the undescribed Carabidae sp. (243). In the macadamia plantation, the 7th and 8th octaves were absent. The most dominant species were the undescribed Harpalini sp. (150, 115b and 126). These 'gaps' may be the result of competition. For instance, high numbers of spiders and ants were also observed in these habitats.

Therefore, the mystery of the missing species reported by Niemela (1993a) is not only peculiar in the boreal environment but also in forests in the southern hemisphere, although further data are required to increase sample size for a better comparison. However, in the macroecological context, species in the southern hemisphere, just as the north, are likely to be regulated by availability of food (Hengeveld, 1980), competition (Niemela *et al.*, 1992a) and the physical environment (Loreau, 1992).

5.7 SPECIES -ENVIRONMENT RELATIONSHIPS

5.7.1 Ordination at the landscape level

Comparative results of the eight sites (section 4.4), in addition to ordinations at the landscape level, produced clear interpretable results. The four forest and four grassland sites situated at high and low elevations broke down to six ecologically-meaningful habitat groups. Recommendations for the conservation of biodiversity in these habitats are discussed in Chapter 6. In addition, this study has shown that local distribution patterns and responses of carabids and cicindelids to environmental factors and to anthropogenic disturbances are similar to those in other parts of the world.

5.7.1.1 Effect of soil characteristics

Along the first axis, natural indigenous mistbelt forest and adjacent managed pine plantation and park at high elevation (900 m.a.s.l.) separated from *Acacia*-dominated woodland, macadamia plantation, hayfield and road verge grassland at lower elevation (700 m.a.s.l.). Along the second axis, the road verge grassland at high elevation separated from the rest of the habitats. The first canonical axis was a pH gradient and the second axis was a moist soil/sand gradient. From the CCA ordination diagrams, species preferences along these environmental gradients and in individual habitats were distinct. It is clear from these diagrams that there are eurytopic species (those in the centre of the diagrams), stenotopic species, forest species and grassland ones.

These findings clearly support several studies of ground beetles in the northern hemisphere which have shown that particular land cover types have characteristic ground beetle faunas (Hengeveld and Hogeweg, 1979; Luff *et al.*, 1989; Turin *et al.*, 1991; Niemela and Halme, 1992). Habitats were classified on their ground beetle assemblages leading to the recognition of

ecologically-meaningful habitats e.g. forest, woodland, grassland, riverside, coastal and marsh. At a higher scale, carabid data from 638 heath and grassland sites in northern and central Europe were classified by TWINSpan, resulting in the identification of 17 habitat groups (Eyre and Luff, 1990a). Some habitat types were confined to the UK, some to continental Europe and some throughout Europe, particularly to wet habitats. Ordination indicated that the greatest difference in species assemblages shown by the first axis was between polders and high-altitudes sites, the second axis was related to soil water and the third axis was related to altitude or to differences between heath and grassland.

The species-environment relationships in this study have shown that local distribution patterns and responses by carabids and cicindelids to environmental factors and anthropogenic disturbances are similar to those of the northern hemisphere. This study has shown that soil characteristics especially pH, moist soil/sand and twig and/or leaf litter determine carabid and cicindelid species occurrence. Land-use and management regimes influence these patterns. The effect of altitude is masked by the presence of soil characteristics in a multivariate analysis, and more so in the presence of pH and moist/sand gradients from one altitude to the next. In the absence of soil characteristics or in a univariate analysis, the altitude factor then appears to be very important. Altitude has therefore an indirect effect on species occurrence in that it determines climate, which in turn determines soil and vegetation type.

In a ruderal ecosystem in Berlin where vegetation in all plots was relatively homogenous and there were no significant correlations between vegetation and numbers of beetles caught, there was a significant correlation between the distribution of five out of 15 aggregating species with pH values (Gruttke and Weigmann, 1990). Yet the pH-values in the topsoil of this relatively homogenous habitat ranged only between 5 and 7. Gruttke and Weigmann, (1990) were not able to ascertain whether this was due to a real relationship or due to chance. The study here confirms the importance of pH of the topsoil in determining carabid assemblage character.

Eyre *et al.* (1986) preliminary work in grassland indicated that factors such as moisture and sand content of the soil affect the carabid communities in grassland habitats, as was the case here.

The importance of dead and decaying trees and soil moisture have been reported as the critical resource for a carabid species *Platynus mannerheimi* within boreal forest which is adversely

affected by logging (Niemela, 1997). This study has shown that litter from decaying trees, twigs and leaves is a critical resource for many carabid beetles associated with forest habitats. These resources have been shown to be important not only to carabids but also to other invertebrates such as saproxylic beetles which also harbour specialist or rare species (Esseen *et al.*, 1992; Siitonen, 1994; Siitonen and Martikainen, 1994 ; Kaila *et al.*, 1997).

Carabid occurrence is partly related to various detectable and often measured environmental variables operating on different spatial scales (Lovei and Sunderland, 1996). Niemela (1996a), has pointed out that sometimes it is possible to pinpoint the exact factor, e.g. soil moisture, but this often fails because the variables are confounded or information about the crucial ones is not measured. Moreover, factors operating on one ecological scale may have little or no explanatory power at another level (Niemela, 1990). For instance, soil moisture may be very important in determining carabid distribution within an old-growth forest stand (Niemela *et al.*, 1987) but the overall availability of suitable forest patches may be decisive for species survival on a regional scale (Niemela *et al.*, 1994a; Haila *et al.*, 1994).

Many authors (Thiele, 1977; Eyre and Luff, 1990a,b; Luff *et al.*, 1992) consider that carabid beetles and invertebrates in general (Kremen *et al.*, 1993) are sensitive and accurate indicators of the state of the environment. Among invertebrates, physical environmental factors seem to shape the species assemblages more than biological relationships such as competition, predation and parasitism (Schoener, 1986). Because they have been widely studied, carabid beetles are a good model group to reveal hierarchical interactions and structures at different spatial scales (Dufrene and Legendre, 1997).

5.7.1.2 Effect of land-use\ management

It has been shown in the northern hemisphere, that particular land cover-types have characteristic ground beetle faunas. The main determinants of the fauna seem to be soil moisture, distance from running or standing water, altitude and vegetation cover. If the distribution of cover type is known, species distribution can be modelled (Luff and Woiwod, 1995). Although the type of land use at any location will clearly affect the diversity and species composition, many land use changes involve variations in intensity within a cover type rather than from one cover type to another. Within intensively-managed grasslands in northern England and southern Scotland, the

carabid fauna was determined primarily by altitude and soil based parameters such as water content, bulk density and amount of organic matter (Eyre *et al.*, 1990). There was a significant effect of pesticide application but this was relatively minor. Within a range of crops, the crop type seems to be more important than pesticide usage in determining the carabid assemblages as the year to year effects were more important than the management system (Booij and Noorlander, 1988). Overall however, organic farming systems seem to support more carabids than conventional ones, due to a combination of increased prey availability, reduced disturbance and greater weed cover (Luff, 1987; Booij and Noorlander, 1992).

The responses of individual carabid species to grassland management intensity have been analysed by ordinating and scoring the various management characteristics (Rushton *et al.*, 1990a). The probabilities of occurrence of various carabids were then related to this management variable by logistic regression, showing responses to intensity of management that were negative (large, non-flying species), positive (smaller, highly mobile species), or which showed an optimum, intermediate management intensity.

Management of scrub and woodland habitats also influences the ground beetle fauna. Scrub management on the Castor national nature reserve affected the ground beetle communities through the extent of bare ground and grass tussocks in the resulting habitat (Rushton *et al.*, 1990b). Within managed forests, there are clear changes in the carabid assemblage, following the cycle of cutting and replanting or depending on the stand composition (Niemela *et al.*, 1993). Any changes in these management practices will thus influence the beetle community present. Any disturbance to the established forest generally increases the carabid diversity in the resultant cleared or scarified areas, although such increase may be short lived (Parry and Rodger, 1986).

Rushton *et al.* (1990a) showed that ordination and logistic regression may be useful tools for modelling the ecological effects on ground beetle communities of qualitative site attributes such as management that are otherwise difficult to quantify and interpret. They noted that management characteristics influence environmental variables, such as soil-water content, that are known to affect the distribution of carabid beetles (Eyre *et al.*, 1986). They also noted that modelling the effects of these variables individually is unrealistic if there is a need to understand the effects of management on carabid beetle species. The relationship between number of carabid species to the grassland management variable (which is equivalent to the level of habitat

disturbance) was carried out using logistic regression (Ter Braak and Looman, 1986). Species showing a negative sigmoidal response indicated a strong preference for unmanaged sites; a positive sigmoidal response showed a preference for intensively managed sites; a gaussian response indicated a preference for intermediate levels of management; and no significant response indicated that the management variable is not important in influencing the distribution of the species on the sites.

5.7.1.3 *Effect of habitat type*

The nominal environmental variable 'habitat type' used here and which was a human-defined classification of the eight sites, could not explain species patterns. Therefore, this study in a way supports the findings of Rykken *et al.* (1997) who have reported that human-defined ecological land types at certain scales are not ecologically meaningful to carabids. The eight human-defined landscape types in this study were classified and ordinated to six ecologically meaningful habitats for carabids. Therefore, for a landscape classification system to be useful for monitoring or predicting biodiversity, it should strike a balance between units that are easily recognizable by ecologists and resource managers, and units that are ecologically meaningful to a variety of organisms (Rykken *et al.*, 1997).

Ecological land classification seeks to impose order on natural landscapes by dividing them into useful and meaningful ecological units. This multi-factor approach to classification attempts to integrate climate, physiography, soils, and biota by describing their composition, structure, and interaction at different geographic scales (Bailey *et al.*, 1978; Rowe and Sheard, 1981; Spies and Barnes, 1985).

In the USA, an ecological classification system has been designed by the US Forest Service (Avers *et al.*, 1993). The classification has eight hierarchical levels, whose land units range in scale from global to local. The aim is to enable national forest departments to adopt the relevant scales of this classification system for the land that it manages and that the mapped ecological units will then serve as a basis for biodiversity assessment, resource management, and conservation strategies. Avers *et al.* (1993) pointed out that species and community distributions can often be related to ecological units, which can be useful in their inventory and protection. Whether or not specific taxa actually recognize physical boundaries of multi-factor classifications

has been little tested.

For instance, ecological land classification was initiated on Vermont's Green Mountain National forest where 583,404-ha forest was divided into nine land type associations (LTAs), based on broad landscape characters such as climate, elevation, and geologic features. These LTAs were then sub-divided into about 80 ecological land types (ELTs). At this scale, land units range from tens to hundreds of hectares and are defined primarily by landform, substrate, soils, drainage and vegetation. There are over 1500 ELTs mapped and classified under this system.

Rykken *et al.* (1997) carried out a study to assess whether the Green Mountain National Forest's classification system in Vermont ordered the landscape into units that are meaningful to a diverse family of forest invertebrates. Ground beetles captured in pitfall traps were compared within and among three human-defined ecological land types to determine if beetle distributions can be linked to an ecological classification system designed to reflect biological diversity. Results indicated that ground beetle distribution were not significantly linked with ecological land types and that the ground beetle fauna of the mid-elevation forests of the western green mountains is comprised mainly of forest generalists, with some specialist species responding to a moisture gradient at the site scale. Because the ecological land type units did not explain distributions of carabids, Rykken *et al.* (1997) suggested that these organisms should next be related to higher and lower scales within the classification system. Therefore, if a landscape classification system is to be useful for monitoring or predicting biodiversity, it should strike a balance between units that are easily recognizable by ecologists and resource managers, and units that are ecologically meaningful to a variety of organisms (Rykken *et al.*, 1997). This study and that of Dufrene (1990 see section 5.3.1) support these findings. Also, Niemela *et al.* (1986a); Niemela (1990); Gruttke and Weigmann (1990) found aggregated dispersion to be typical among carabid species of woodland habitats. For these authors, vegetation structure also provided no or insufficient evidence for the interpretation of dispersion patterns of the most species.

In a recent review by McGeogh (in press), on the selection, testing and application of terrestrial insects as bioindicators, it has been reported that, "Rykken *et al.* (1997) actually reject the use of ground beetles as indicators of land-type diversity in Vermont after the outcome of ordination and classification analyses". This statement is misleading, because it gives the impression that ground beetles are not indicators of land-type.

What Rykken *et al.* (1997) reported is that human defined land-types may not always be recognised by carabids. In addition, even though data analyses was based on spring sampling only and no environmental variables were measured or related to species patterns, results of the ordinations by DECORANA still suggested that the distribution of ground beetles was somewhat influenced by site moisture.

Also classification by TWINSpan separated groups of hygrophilous species and wet sites and several of the site-groups contained sites affiliated primarily with one ecological land type, even though sites considered in their study occur across an apparently homogenous northern hardwood forest landscape, where site-scale habitat heterogeneity may be very subtle. Therefore, their (Rykkken *et al.* 1997) results indicated that ground beetle distribution were not significantly linked with ecological land types and that the ground beetle fauna of the mid-elevation forests of the western green mountains is comprised mainly of forest generalists, with some specialist species responding to a moisture gradient at the site scale. It is therefore important to define scale in the use of bioindicators.

The influence of spatial scale on species richness relationships is pervasive and biodiversity indication studies cannot afford to ignore scaling effects (Hammond, 1994; Niemela, 1996b; Rykken *et al.*, 1997). Larger spatial-scale disturbance effects are inclusive of the scales below them. For instance, the impact of a disturbance at the smallest level of a single habitat unit of an individual organism, in which case bioindication procedures may be macro-molecular or organ based, e.g. heavy-metal contents of insect tissues or number of ovarioles in female individuals (Kroupa *et al.*, 1990). However, when a disturbance operates at a larger local, regional or global scales, bioindication procedures may also involve the measurement of parameters associated with species populations or communities or higher level taxonomic groups (Noss, 1990).

The spatial scaling restrictions on the choice of a bioindicator are thus the distribution of the species or group and the presence of suitable habitat within the area in which it is required as an indicator. The objective of bioindicator selection is then to identify the organism or group of organisms below this scale of stressor or disturbance incidence, and at the scale of interest, that readily respond to the stressor/disturbance or in the case of biodiversity indicators reflect the diversity of other taxa (McGeogh, 1998).

To test further, the utility of ecological classification system (Rykeem *et al.*, 1997), there is also a need to study the distribution of other invertebrate and vertebrate species. Only in the context of other groups of organisms are the features that make carabids special thrown into relief (Hammond, 1990). Carabids share the generalist, surface-active predators guild with at least some spiders, ants (Niemela, 1990, 1993b; Niemela *et al.*, 1996), Staphylinidae and Opiliones whose numbers usually play similar or complementary roles to ground beetles in addition to being polyphagous predators in agroecosystem (Hammond, 1990). Lawton *et al.* (1998) have warned that, no one group serves as a good indicator taxon for changes in the species richness of other groups. This, stresses the need to understand the ecology of all taxa for better informed decisions in the planning of biodiversity conservation.

5.7.2 Ordination of point habitats

Ordination at the level of point habitat was able to better separate or characterize within-habitat variations based on sum of two-year species data than single year species data. This result again stresses the importance of collecting data over at least two seasons for meaningful conclusions. Provided that there are sufficient replicates over time, pitfall captures of these animals can be used to characterize the various site types and disturbances both at the level of site and of point habitats.

Within each site, the most dominant species reached maximum abundance in certain point habitats. Therefore, individual species were not randomly distributed among the traps but occurred in aggregations and were associated with certain microhabitats. For example, in the park there was high species abundance under stones used for landscaping and under trees providing leaf litter and shade. High species abundance occurred in the road verge point habitats after burning and/or cutting of the grass. In the macadamia plantation, high aggregated abundance was among heaps of leaf litter, and in the *Acacia*-dominated woodland there was high aggregated abundance of the undescribed Harpalini sp. (35b) among the wet, sandy shores of an intermittent river. This result is a clear indication of the need for heterogeneity of individual sites which increases variation in population distributions within sites. This study supports the maximization of these microhabitats at the local scale as an appropriate conservation strategy (see details in Chapter 6). This also supports findings in the northern hemisphere that certain species prefer particular microhabitats (Middleton and Merriam, 1985; Niemela *et al.*, 1988;

Niemela, 1990).

Ground beetles generally show non-random, spatial distributions both within and between habitats (Luff, 1986; Niemela, 1990; Niemela and Halme, 1992). Studies on increasingly fine scales have shown that distributions of European carabid species are generally structured with respect to habitat patches within forest types (Buse, 1988; Niemela *et al.*, 1988) and even within the movement range of individual beetles (Hengeveld, 1987; Niemela and Halme, 1992; Niemela *et al.*, 1992a).

5.8 IMPORTANCE OF USING TWO ORDINATION METHODS

Ludwig and Reynolds (1988) recommend the use of more than one ordination method on a data set. CA and MDS are well-suited for studying species distributions from several sample units (Ter Braak, 1985; Clarke and Warwick, 1994). The DCA algorithm has been criticized (Warternberg *et al.*, 1987; Jackson and Somers, 1991; Clarke and Warwick, 1994) and it has been shown that results obtained with DCA vary depending on the number of segments used to remove the arch effect. Therefore, several runs with different numbers of segments must be done to find stable factorial axes and interpretable results.

On the other hand, PCA is not generally used on species data (Ter Braak, 1988; Ludwig and Reynolds, 1988; Jongman *et al.*, 1987). CA or DCA are often advocated (Hill and Gauch, 1988; Ludwig and Reynolds, 1988). However, Debinski and Brussard (1994) found CA had problems with distortions at the ends of the axes and since DCA has been criticized, they used PCA. The 'arch effect' seen in PCA of their data was in fact an accurate representation of the data.

Similarly, in this study, ordinations of species data of the first sampling season arranged for the eight samples and 32 point habitats for individual seasons did not give interpretable results using CA, DCA and MDS ordinations e.g. (Fig. 4.12b), but PCA ordination on the same data gave meaningful interpretable results. The results of both CA and DCA were found to be less than 1.5 standard deviations and it was therefore safe to use PCA (Ter Braak, 1988). PCA can be performed on binary data, provided that association tests based on assumptions of normality are avoided (Green, 1979).

In addition, the methods used to link species patterns to environmental variables in the two

programs, produced ordination diagrams that separated the eight sites in a similar manner and isolated the identical most important environmental variables responsible for the observed species patterns. The only difference was in ordering the most important soil characteristics. In order of importance, PRIMER listed them as pH, sand, litter and moisture, and CANOCO listed them as pH, litter, moisture and sand. However, since these variables are highly confounded in nature and are all related to soil (either positively or negatively correlated), both results are acceptable.

Although PCA option (for species data) is not available in PRIMER (1994), PRIMER was found to be more user friendly than CANOCO (1994). On the other hand, ordination diagrams produced by CANOCO give more information in one diagram (samples, species, environmental variables). However, both methods were adequate for analysing the data here, and any of the two methods could have been used. Therefore, CANOCO or PRIMER can be used depending on how one wishes to present the data.

5.9 SIGNIFICANCE OF FINDINGS IN A MACROECOLOGICAL CONTEXT

This study here in South Africa and those carried out in Finland and Canada (Niemela *et al.* 1993) show the feasibility of a multi-regional approach. These studies show that although species identities differ between the three continents, the general patterns of community response to human caused disturbances are surprisingly similar.

The macroecological approach can also be used as a management tool distinguishing between local effects and general global effects. For example, in Europe, only small sized carabid species survive frequent disturbance (Sustek 1992; Blake *et al.* 1996) and the same has been found here.

Many studies have shown that carabids are sensitive to environmental changes and will thus signal human caused disturbances (Pearson and Cassola 1992, Niemela, 1996, Luff, 1996). This study supports the use of carabids in biodiversity assessment. It also supports the use of carabids in monitoring programmes to determine the effects of management and refine it as needed. Monitoring is recognised as an integral part of efforts to use the earth's biological resources sustainably.

This study indicates a great potential to utilise ground beetles as a tool for assessing landscape

changes on an international scale. In view of the landscape changes that human activities cause across the world, a global programme that uses the same taxonomic group in visually-similar land-mosaics but in different parts of the world is needed. Carabids are taxonomically and ecologically abundant and sensitive to environmental changes to be a reliable signal of human-caused disturbances (Niemela, 1996; Dufrene and Legendre, 1997).

For instance, Table 5.1 lists sampling methods, mainly pitfall trapping, of some studies similar to the one here, but carried out in the northern hemisphere, in visually-similar habitats (forests and grasslands) to determine the response of carabids to anthropogenic disturbances. Inevitably, there have been and will be minor differences in methodology in the different studies, but nevertheless the overall results are comparable. For example, in Table 5.1, sampling of habitats with traps of various mouth diameters, different collecting preservatives, periods of collecting ranging from tens of days either during spring and or summer to three annual seasons have led to interpretable results. Nevertheless, it is shown in this study and that of Maelfait and Desender (1990) that studies involving short periods of sampling should best be interpreted by specialists of the animals concerned.

This study has used the macroecology approach to compare patterns and responses of carabids to various landscape disturbances in the southern hemisphere with those in the northern hemisphere. The findings in this study (see also Chapter 6 and 7), indicate that indeed the macroecology theory is useful and has a great application.

No.	Place	Habitat (sites)	Trapping design		Trap type				
			design	total traps	capacity	mouth diameter	shape	material	collecting fluid
1	Pietermaritzburg South Africa	4 forests & 4 grasslands	stratified sampling 16 pitfall traps x 8 sites.	128	240 ml	7.5 cm	circular	PVC	ethylene glycol
			4 window traps / site.	32	-			glass	
			4 PVC-netting traps/site.	32	-			PVC- netting	
2	Alberta, Canada Niemala <i>et al.</i> , 1992	4 forests & 1 meadow	4 x 4 grid (5m by 10 m apart) 16 traps/site	80	1-litre	10 cm	circular	PVC	none
3	Vermont, U.S.A Rykken <i>et al.</i> , 1996	3 forests (ecological land types- ELT)	nested design 90 traps /ELT	270	10 cm deep	8 cm	circular	PVC	0.05% formalin
4	Aland Islands, SW Finland Niemela and Halme, 1992	cultivated, abandoned fields, pastures and forests	3x5 grid/site 15 traps /site 17 forests 51 other sites	1020	170 ml	6.5 cm	circular	PVC	detergent and water

Table 5.1: List of sampling methods of some studies similar to the one here, but carried out in the northern hemisphere, in visually-similar habitats (forests and grasslands) to determine the response of carabids to anthropogenic disturbances.

No.	Place	Mode of operation	Total No. of trapping days	Period of collecting	No. of seasons	Total individuals	Total species
1	Pietermaritzburg, South Africa	Pitfall traps open 30 days/month.	2 years.	1994-1995 (June-May) 1995-1996 (June-May)	2	4197	37
		glass window.	6 months	1994/1995 (September-March)	1	4	2
		PVC-netting.	6 months.	”	1	0	0
		visual-searching.	10 months.	1994-1996 (October-February)	2	254	19
2	Alberta, Canada Niemala <i>et al.</i> , 1992	traps open 1 day/week	17 days	1981 (May-October) 1982 (May-september)	2	2310	54
3	Vermont, U.S.A Rykken <i>et al.</i> , 1996	traps open for 30 consecutive days	30 days	1994 (June-July)	1	9041	35
4	Aland Islands, SW Finland Niemela and Halme, 1992	traps open for 10 days	18 days	1994 (May-August)	1	4901	77

Table 5.1: Continued.

No.	Place	Habitat (sites)	Trapping design		Trap type				
			design	total traps	capacity	mouth diameter	shape	material	collecting fluid
5	Southern Finland (taiga) Niemela <i>et al.</i> , 1992	1 forest	12x25 grid (5 m apart total area 1.3 ha)	300	170 ml	6.5 cm	circular	PVC	Sodium hydroxide solution
6	Southern Finland Niemela <i>et al.</i> , 1988	old and managed coniferous forest	3x5 and 5x6 grid 15-30 traps/site. Supplemented by hand-picking, sieving and sweep-netting	1230	170 ml	6.5 cm	circular	PVC	detergent and water
7	Western Canada Niemela <i>et al.</i> , 1993	boreal forest 10 mature and 10 regenerating stands	Traplines with 6 traps/site	120	-	10 cm	circular	PVC	ethylene glycol
8	North East Netherlands Vermeulen, 1993	Road verges and adjacent open heathy areas.	Trap series for hundreds of metres.	149	-	10 cm	circular	PVC	4% formalin

Table 5.1: Continued

No.	Place	Mode of operation	Total No. of trapping days	Period of collecting	No. of seasons	Total individuals	Total species
5	Southern Finland (taiga) Niemela <i>et al.</i> , 1992	traps open throughout the season and serviced every 5 days	6 months	1985 (May-November)	1	2405	22
6	Southern Finland Niemela <i>et al.</i> , 1988	traps open 5/8 days.	13 days.	1984 (June/August)	2	422	22
		traps open 21/15 days.	36 days.	1985 (June/August)		1564	40
		hand picking and sieving.	350 working hours.	1985 (June)	1	54	10
		Sweep-netting.	300 sweeps	1985 (June)	1	0	0
7	Western Canada Niemela <i>et al.</i> , 1993.	continous pitfall trapping emptied every 14 days.	139 days	1989 (May-October)	1	5738	53
			173 days	1990 (May-October)	1		
			140 days	1991 (May-October)	1		
8	North East Netherlands Vermeulen, 1993.	continous pitfall trapping emptied every 2-3 weeeks	7 months x 3 years	1989 (April-October) 1990 (April-October) 1991 (April-October)	3	-	29

Table 5.1: Continued

No.	Place	Habitat (sites)	Trapping design		Trap type				
			design	total traps	capacity	mouth diameter	shape	material	collecting fluid
9	England Eversham and Telfer, 1994	Road verges	trap transects (400 m). Direct searching.	50	8 cm deep	7 cm	circular	PVC	20% ethylene glycol
10	Central Italy Comandini and Taglianti, 1990	Mediterranean woodland and pastures.	6-10 traps x 9 sites	72	11 cm deep	9 cm	circular	PVC	-
11	Berlin Germany Gruttke and Weigmann, 1990	Suburban ruderal ecosystem	10 traps 2 m apart x 1 site)	10	-	7 cm	circular	PVC	3% formalin and detergent
12	Berlin, Germany Kegel, 1990	Urban ecosystem (street margins, yards)	10 traps x 21 sites	210	-	-	-	-	4% formalin solution
13	Southern Belgium Dufrene and Legendre, 1997	Natural and subnatural open habitats	10 traps x 69 sites	690	1.25L	-	circular	PVC	5-10% formalin solution

Table 5.1: Continued

No.	Place	Mode of operation	Total No. of trapping days	Period of collecting	No. of seasons	Total individuals	Total species
9	England Eversham and Telfer, 1994	continous pitfall trapping.	25 days	1993 (March-October)	1	1172	35
		Direct searching	32 hours			-	66
10	Central Italy Comandini and Taglianti, 1990	continous pitfall trapping emptied every 30 days	-	-	-	-	57
11	Berlin Germany Gruttke and Weigmann, 1990	continous pitfall trapping	9 months x 3 years	1982/1984 (April-December)	3	-	68
12	Berlin Germany Kegel, 1990	-	3 months	1983 (April-June)	-	5147	77
13	Southern Belgium Dufrene and Legendre, 1997	continous	3 year cycles	1986/1987	3	39984	189

Table 5.1: Continued

CHAPTER 6

RECOMMENDATIONS FOR CARABID AND BIODIVERSITY CONSERVATION MANAGEMENT

6.1 AIMS OF MANAGEMENT

Consensus is emerging among ecologists that biological diversity will not be conserved effectively in natural reserves alone. The existing reserve network is too small, major expansion is unlikely, and barriers to migration make species in reserves especially vulnerable to global climate change (Wilcove, 1989; Westman, 1990). It is recommended that reserves be complemented with a matrix of semi-natural lands where ecological principles are used to manage both for commodity production and conservation of species diversity (Harris, 1984; Hansen *et al.*, 1991). The challenge is now to design and effectively manage such multipurpose landscapes.

Invertebrate home ranges are generally small (Ehrlich, 1992), and many invertebrates have clear microhabitat requirements (Niemela *et al.*, 1987; Kaila *et al.*, 1997; Siitonen and Martikainen, 1994). A central aim of a management strategy for carabids and cicindelids, and for biological diversity in landscapes, is to maximize the creation and maintenance of these microhabitats.

The single most important cause of insect species extinction is the destruction of natural habitats (Pyle *et al.*, 1981). In disturbed landscapes, we can only attempt to approximate the pristine human, pre-settlement condition, and this new landscape will not manage itself (Noss, 1983). Species composition and abundances assume primary importance in the context of regional conservation. The proportion of localised versus widespread species is important when deciding whether conservation is for rarity or for typicalness (Samways, 1994). Where conditions allow, management should focus on rare species, and insulate species with high extinction probabilities. On the other hand, single-species efforts should not compromise conservation for numbers (Ehrlich, 1992), or for ecological processes.

This is the first study to be carried out on carabid assemblage patterns and responses in natural habitats and agricultural ecosystems in southern Africa. This chapter now makes suggestions for management of carabid and cicindelid diversity in the region.

6.2 IMPLICATIONS FOR CONSERVATION MANAGEMENT

The main management recommendations that have come out of this study are as follows:

6.2.1 Forests and woodlands

The environmental objectives for the management of forest landscapes must ensure that forests are capable of producing biological raw materials of a high quality on a sustainable basis, while preserving their biological diversity and cultural historical features. Among other things, this objective means: (i) that the biological functioning and nutrient status of forest soils should provide a basis for sustainable production; (ii) that viable populations of plant and animal species naturally associated with forests are able to survive; (iii) that threatened species and habitat types are protected; (iv) that exotics and invasive species which threaten biodiversity are controlled and /or not introduced; (v) and that the social values of forests are safeguarded (Franklin, 1989; Esseen *et al.*, 1992; Bradshaw *et al.*, 1994; Korhonen, 1994; Noss and Cooperrider, 1994).

To achieve these aims, it is important to ensure: (i) that forestry methods are more carefully adapted to local site conditions; (ii) that there is an increase in the area of protected forest; (iii) that there is avoidance of any losses of key habitats; (iv) promotion of wider use of natural regeneration on suitable land; (v) retain more dead wood in forest; (vi) preserve remaining natural forests; (vii) improve conditions for the survival of threatened species, (viii) take greater account of large-scale landscape patterns and reduce fragmentation; (ix) set aside large natural areas and environments of significant biological and cultural historical interest; (x) ensure greater reuse of wood fibre (Franklin, 1989; Esseen *et al.*, 1992; Bradshaw *et al.*, 1994; Korhonen, 1994; Noss and Cooperrider, 1994; Niemela, 1997). These methods are now being practised in some areas, especially in boreal forests (Niemela, 1997).

Invertebrates are important in the biological functioning and maintenance of the nutrient status of forest soils. In addition, Niemela (1997) has pointed out that invertebrates have potential utility as a surrogate for biodiversity, yet they are rarely used in conservation studies.

This study showed that, although the composition of species between a natural moist indigenous forest and adjacent pine plantation was very similar, there were three species (*Lebia nematopeza insidiosa*, *Systolocranius alternaris* and *Hystrichopus atratus*) recorded in natural moist indigenous forest but not in pine plantation. From comparative boreal forest studies of Niemela *et al.* (1988) in Finland and Niemela *et al.* (1993) in Canada, and from a macroecological comparison, it appears that South African natural indigenous forest must be serving as a source of species for recolonization of exotic pine plantations after logging in addition to providing microhabitats for these specialist species. Although, *L. insidiosa* and *H. atratus* were recorded in other forest habitats such as macadamia plantation with intensive irrigation (only *H. atratus*) and in point habitats near a river in *Acacia*-woodland particularly (both species), means that high soil moisture and litter appear to be a critical resource for these species. Indeed, CCA results showed that, in addition to soil pH and moisture, availability of litter was important for certain species and various types of management or disturbances influenced these factors.

The natural indigenous moist forest and exotic pine plantation were 200 m apart. The pine plantation was in the middle secessional stage (i.e. 12 years because mature pine is logged from 25-30 years) and had been pruned once in the first season which was the second pruning at 5m height. The first pruning had taken place at 3m height. Pruning had the effect of increasing leaf and twig litter, in addition to reducing shade cover and increasing herb cover. Both of these conditions, especially the presence of tree branches from pruning, and twig and leaf litter, may have mimicked the litter conditions in the near adjacent indigenous forest which provided preferred habitats for many of the common species found in both forests. It is important that the branches and twigs after pruning should not be cleaned away. In addition, spring and summer burning should be avoided in all forest types and woodlands, because this is the period of maximum insect abundance.

Seasonal population variations showed natural indigenous forest to be a more stable habitat (in terms of population variations from one season to the next) for carabids than was pine plantation. Also, diversity measures showed that the natural indigenous forest had higher species richness, diversity and more rare species than pines.

In a study of the distribution of carabid beetles in fragments of old coniferous taiga and adjacent managed forest, Niemela *et al.* (1988) found that primeval forests and managed forests had

similar carabid assemblages, and that species richness was highest in young plantations. The study here showed that species richness was higher in a natural old (over 150 years) indigenous forest relative to the exotic pine plantation in the middle successional stage (about 12 years) and carabid assemblages were very similar in both forests. This observation of higher species richness in an older forest may be the result of comparing two different forest types and sizes and the edge effect. Therefore, further research is needed to determine carabid assemblages within the interior of the natural indigenous forest, as this study only sampled from 40 m from the edge into the forest. Also, the carabid assemblages of the early and late successional stages of pine plantation stands need to be determined. This study sampled from a one-hectare stand of pine in the middle successional stages and the assemblages of the interior and edge species were similar to the adjacent indigenous forest (250 ha). Niemela *et al.* (1988) found that in general, community characteristics in edges were similar to fragment interiors and species richness was also similar between edges and interiors. The only difference between the edge and interior was that some individual species favouring moist primeval forests were less abundant at the edges than in the interior. In order to detect possible area effects, fragments larger than 30 ha and smaller than 5 ha were compared. No differences were detected in the species-assemblage characteristics, and out of the nine most abundant species, seven were more abundant in the small fragments than in the large ones, and the two species were equally abundant in the two fragment size classes.

The observation of lower species richness in mature forest than in regenerating sites is supported by other studies in the northern hemisphere: Niemela *et al.*, (1988, 1993)-coniferous boreal forest in Finland and western Canada; Jennings *et al.* (1986)-spruce-fir forest in Maine; Arnoldi and Matveev (1973)- Russia; Szyszko (1983)- pine forests in Poland; Sustek (1981)- pine forest in Czechoslovakia and Lenski (1982)-oak forests in the USA. In addition, these studies suggest the following general responses of ground beetles to logging: (1) initially, species typical of open, grassy habitats increase (2) forest generalist decrease but seem to recover with forest regeneration (3) some mature forest specialists fail to recolonize regenerating forest and are at risk of extinction in logged patches. Logging has a consequence of removal of trees and subsequent change in environmental conditions e.g. reduction of soil moisture resulting in dryness of early successional forest stages (Niemela *et al.*, 1993). Secondly, the destruction of suitable habitat patches leads to increased isolation between the remaining ones, decreasing the

likelihood of recolonization (Niemela *et al.*, 1993, 1994a).

In addition to local processes, community composition is determined by regional processes, such as species dispersal and historical events, and by habitat diversity (Ricklefs, 1987). Thus maximization of regional habitat diversity has been suggested as a means of conserving biological diversity (Noss, 1983, 1992; Hunter, 1990; Soule, 1991).

In boreal forest landscapes, it has been suggested that this may be best achieved by ensuring that different forest types and age classes are included in a regional forest mosaic designed with connectivity appropriate for organisms operating on several scales (Harris, 1984; Niemela *et al.*, 1988; Hansen *et al.*, 1991). This study has shown that this should not only be the strategy in boreal forest but also that plantation forestry in the southern hemisphere should follow this approach. Furthermore, prescribed burning could be used to create suitable habitat for any pyrophilous species (Mitchell and Martin, 1980; Franklin, 1988). This study and that of Niemela *et al.*, (1993) support the approach of maximizing habitat diversity as the inclusion of regenerating forest stages into the habitat spectrum increases carabid species diversity. If clear cuts become a dominant landscape element however, they may threaten the existence of mature forest specialists and, in the long run, even the survival of forest generalists, by homogenizing the fauna and ultimately depressing regional diversity.

In this study, the primary natural indigenous forest at Ferncliffe covers an area of 250 ha and is surrounded by plantations of exotic pine and gum. This arrangement ensures that the carabid diversity of planted forest at various successional stages is enhanced as species abundance increases in these habitats, which are, in turn, sustained by the natural forest which acts as a source for the recolonization of new planted forest patches for both generalist and specialist species after logging. Insect populations fluctuate greatly (Samways, 1990), more so in disturbed habitats (Loreau, 1992, 1994; Niemela, 1993a). Because of this, even abundant species have been known to become extinct (Samways, 1990, 1996; Lockwood and De Brey, 1990). This study has shown that natural indigenous forest provided a more stable habitat for carabids with many rare species and high diversity. The need to preserve these natural forests is great. There is therefore a need to promote the regeneration of this forest on suitable land on a regional scale to form a mosaic of patches of natural forest surrounded by planted forest in various seral stages. These cool, tall, inland forests were greatly exploited for *Podocarpus* timber in the past (Pooley,

1993). In addition, indigenous residents harvest these forests for firewood and medicinal plants. What we do not know is what the carabid fauna of Ferncliffe was before it was reduced in size. It may be that it is in a state of faunal relaxation and that being surrounded by exotic trees accentuates this process.

In addition to being important components of ecological webs in forests, invertebrates like ground beetles may also serve as useful indicators of forest condition (Wilcove, 1989). The sensitivity of carabids to environmental variation and their rapid responses to habitat change, (Turin and den Boer, 1988; Desender and Turin, 1989; Niemela *et al.*, 1993), make them candidates as 'indicators' for assessing the effects of habitat change (Eyre and Rushton, 1989; Eyre *et al.*, 1989; Niemela, 1997; Dufrene and Legendre, 1997). In comparison with other taxa, Hansen *et al.* (1991) reported that species richness of vascular plants, fungi, amphibians, reptiles, small mammals, and birds did not differ between natural young successional stages and mature stands in fir forests in the coastal northwest of the USA. Hansen *et al.*, (1991) also found similar bird species richness between plantations and natural mature forest in the coastal northwest USA, and in the Palearctic boreal forest in Finland (Raivio and Haila, 1990). These comparisons suggest that many invertebrates are very sensitive to habitat changes, perhaps because they operate at a smaller spatial and temporal scale than vertebrates (Hafernik, 1992).

In using carabids as bioindicators (Dufrene and Legendre, 1997), sensitivity to different forest types to logging could be estimated by examining their ground beetle composition before cutting. After logging, the extent of change in forest communities and especially their recovery could be assessed by studying the dynamics of species selected as indicators (Niemela, 1997).

Carabids are also excellent subjects for studies of the effects of fragmentation on species with different dispersal abilities and habitat requirements (den Boer, 1990). Although vertebrate taxa have received some attention in this regard (Landres *et al.*, 1988), invertebrate populations are likely to operate on different spatio-temporal scales. If we are seriously interested in the challenge of maintaining biological diversity and ecological integrity of forest systems, we can not afford to ignore invertebrates.

6.2.2 Recreational parks

The obsession with tidiness in recreational parks has had a devastating effect on insect and plant species (Fry and Lonsdale, 1991). Although, insect species from various groups, such as the Coleoptera and Heteroptera (Morris, 1971), Lepidoptera (Dempster, 1971; Thomas *et al.*, 1986), Orthoptera (Marshall and Haes, 1988) and ants (Samways, 1983) depend on some regular disturbance to maintain their population numbers, it is the major disturbances such as ploughing, heavy grazing, fertilizing plots, vertebrate grazing, especially by goats, and recreational pressure that contribute to declining population levels, and loss of local insect populations (Fry and Lonsdale, 1991).

This study has shown that the intensive maintenance of lawns in the park by frequent mowing greatly reduces the abundance of carabid populations, and results in a high turnover of species from adjacent natural forest and pine plantation. However, certain species like *Metagonum gilvipes*, which was abundant in the pine plantation, was also abundant under trees, which provided shade and leaf litter, as well as under large stones in flower beds in the park. Recreational park management should aim at maximising these habitats at the local scale to enhance biodiversity, in addition to applying rotational mowing that has been advocated elsewhere (Morris, 1991). Kegel (1990) showed that, repeated mowing and intensive irrigation leads to drastic changes of abiotic conditions which prevent seed-production of the plants, thus seed-feeding carabid species are eliminated and forest dwelling species increase. This was also shown to be the case for parks and gardens in west Berlin (Kegel, 1990).

6.2.3 Road verge grasslands

Pietermaritzburg by-laws prescribe that grasslands and bush along road verges and within nature reserves be controlled by burning and /or cutting. This reduces the risk of wild fire and bush encroachment. Natural burns on the landscape from lightning strikes are a widespread phenomenon, particularly in savanna areas such as parts of Australia (Gill *et al.*, 1981) and Africa (Samways, 1993). Burning maintains the savanna as grassland, preventing succession to natural scrub (Tainton and Mentis, 1984). In the current annual management by burning of road verges, invertebrates and plants are not considered.

This study has shown that four cicindelid species *Dromica gilvipes*, *D. tuberculata carinulata*,

Cicindela marginella inanis and an undescribed Cicindelini sp. (250b), and carabid species *Graphipterus cordiger subhamatus* and *Callistomimus caffer*, thrive on early successional grassland during spring to mid-summer after autumn burning, while the carabid species *Euleptus caffer* thrives in late succession tall grasses from mid-summer to autumn. In addition, other carabid species, such as the undescribed Harpalini sp. (115b) and Harpalini sp. (35a), reaches maximum abundance in grasslands over autumn. Others like *Metagonum gilvipes* were present all season, particularly in the wider more open areas of road verges. Therefore, in the annual management of these grasslands, where different species require different seral stages, the use of fixed plot or rotational management is recommended to ensure the continual presence of particular plantscapes, such as tall and short grassland essential for the survival of many different plants and animals (Morris and Rispin, 1987; Rushton *et al.*, 1990b). Burning during late spring and summer should be avoided, as this causes high carabid mortality. Instead, burning should take place in autumn or winter.

The temporal appearance of carabid and cicindelid species, particularly in the road verge grasslands, is dependent upon some disturbance, especially burning and cutting. However, when the burning is extensive, such as several kilometres, without leaving islands of unburnt grass, this may destroy preferred habitats for some species leading to a decrease in numbers and species. Therefore, to enhance diversity of all species, management should involve burning grasslands every autumn, within which islands of unburnt grass must be present. This rotational burning would maintain a plantscape of various successional stages and provide a variety of preferred habitats for many species.

Seasonal effects of management are important for the fauna and flora of grasslands (Morris, 1971). Traditionally, most methods of managing grasslands are applied at a particular time of the year because they have been derived from agricultural practices which had nothing consciously to do with biodiversity conservation. Thus mowing for hay tends to be done in early summer, and burning in late autumn or spring when the vegetation is neither full of sap (and being grazed) nor sodden with winter rain. Grazing has normally been practised at all times of the year because stock has to be fed throughout. If management treatments are applied annually, it is inevitable that effects will be produced on populations of most invertebrates animal (Morris, 1971, 1991, 1990a,b; Morris and Rispin, 1987; Rushton *et al.*, 1990). Thus summer grazing will

reduce the numbers of floral and other aerial structures, in particular plant species, and will lower the general height of the vegetation, while winter grazing will interfere with overwintering populations of animals (Morris, 1991). The importance of time, particularly in relation to the phenology of both plant and animal species, needs to be emphasized. Wells (1971) has related the phenology of flowering of chalk grassland plants to management, and pointed out how the timing of management can encourage differentially the seed production of species which flower at different seasons. Therefore, the conservationist needs to be able to recommend a particular time of year for treatment, if an annual treatment must be applied. The conservationist also needs to demonstrate the effects of management at different times of the year on certain species of invertebrate animals, the representation of species in particular taxonomic groups, and, if possible, on animal communities. Rotational regimes of management have been recommended as being the best method of preserving and enhancing faunal richness in nature reserves (Morris, 1991). Essentially, rotational regimes maintain different successional stages simultaneously in time, so that species and associations of species are represented. Management can be by burning, mowing or grazing, which are known to produce an interesting succession of invertebrate animals (Morris, 1971, 1991). Coincidentally, Chambers and Samways (1998) showed that at sites close to the carabid sites in this study, maintenance of high grasshopper diversity also depends on rotational management. Fire initially deprives, for example, grasshoppers of food (Gandar, 1992). However, elevated post-burn soil temperatures, through increased insolation, allow some grasshopper nymphs to emerge earlier than usual, which, coupled with more nutritious vegetative regrowth, progressively increases grasshopper populations. Some beetles even depend on fire and have highly developed tactic response to smoke to locate burnt trees in which to lay their eggs (Mitchell and Martin, 1980).

Cicindelid species made up only 2.6% of the total catch here. They occurred in burnt or cut grassland road verges. Cicindelids are habitat-specific, and more so than most carabids. The road verges studied here were found to have soils with high sand content and low moisture thereby, providing a special microhabitat for many xeric species. The four cicindelid species recorded (*Cicindela marginella inanis*, *D. tuberculata carinulata*, *D. gilvipes*, undescribed Cicindelidae sp. 250b) and the carabid species *Euleptus caffer* and *G. cordiger subhamatus*, can be used both as indicators of disturbance and particular levels of biodiversity in sandy road verge grasslands. Indeed, this site had high species richness and diversity (H') in the eight sites studied

in addition to having many rare species. This fact is also supported by results from x2 geometric plots and suggestions from Dutrene and Legendre (1997) (see section 5.5.3) that these species are likely to be bioindicator species of this site. It is therefore suggested that if these animals are found to be absent from these sites on monitoring over two seasons, it should signify the presence of stress resulting from poor fire management of these sites. These species can also be considered as good indicators of biodiversity of a minimal width of 20 m of sandy road verges studied. The study was carried out over a range of 20 m to 100 m wide along a 500 m stretch.

Comparison of species in road verges between this study and those in the northern hemisphere, particularly Vermeulen (1993) and Eversham and Telfer (1994), showed that there is no similarity between species listed in these studies and those recorded in a sandy road-side site here. However, the only similarity is at the genus level (*Cicindela*) species. Vermeulen, (1993) recorded three species *Cicindela hybrida*, *C. sylvatica* and *C. campestris*. In this study, *C. marginella inanis* was recorded. Vermeulen (1993) also reported that the species *C. hybrida* was frequently observed visually, although it was hardly caught in pitfall traps because it is a very good flyer. The same observation can be said of *C. marginella inanis* in this study. This may also be the reason why it was one of the two species caught by glass window traps.

Further comparative studies carried out in the northern hemisphere, especially in the Netherlands (Vermeulen, 1993, 1994), showed that sandy road verges may aid the survival of stenotopic Carabidae associated with open habitats such as heathland and sandy grassland. It was suggested that road verges serve as corridors linking heathland fragments, thus maintaining a metapopulation structure which helps avoid regional extinction. However, Eversham and Telfer (1994) argued that the verges encourage dispersal into unsuitable habitats and function as sinks in which individuals die without reproducing. They found stenotopic species recorded from road verges but not in adjacent open habitats all had high powers of dispersal. The least successful dispersers were found only in open habitats and in verges closely connected to them. This supports the concept of road verges acting as corridors. They also found that stenotopic species were breeding on the road verges which therefore functioned as refugia rather than corridors.

The findings here support those of Eversham and Telfer (1994) because the four cicindelid species recorded here were good fliers, which improves their dispersal ability. In contrast, carabid species which did not fly were recorded in higher abundance in the more open road

verge habitats with a very wide width. This suggests sandy road-verge grasslands subjected to alternating annual autumn burning provide preferred habitats for stenotopic carabid and cicindelid species, and they function as a dispersal corridors as well as breeding refugia. For example, the Graphipterinae species *G. cordiger subhamatus*, which is usually found in high abundance in the drier, western part of the southern African region, was found in the open burnt and cut sandy areas along road verges in this study in a wetter part of the region. The cicindelid species *D. gilvipes* was recorded at another road verge at lower elevation only after fire disturbance. Therefore, implications for the conservation for biodiversity of this road-verge grasslands are clear: for carabids and cicindelids dependent on early successional habitats, survival may be more likely on disturbed roadside verges than in nature reserves in the absence of regular management disturbance.

Furthermore, Eversham *et al.* (1996) have shown that man-made sites in Europe, such as sandy road verges, are analogues of natural habitats for carabids. These road verges not only support eurytopic species which occur in the surrounding landscape, but also support a stenotopic (rare and threatened) component comprising colonists from seminatural habitats. Therefore, the survival of species once they have reached man-made sites will depend on how closely the site matches the environmental conditions of the seminatural equivalent. This study has shown that the prescribed disturbances of burning and mowing produce bare ground and successional stages, which are particularly valuable to both stenotopic and eurytopic carabids. Although roads and railways have the potential both to divide and fragment seminatural habitats, they also link them (Vermeulen, 1993, 1994; Eversham and Telfer, 1994). Therefore, based on the findings of this study, it appears that road verges in the southern hemisphere also have high conservation value. Samways *et al.* (1997) in South Africa and Keals and Majer (1991) in Australia have also shown this to be the case with ants.

6.2.4 Agriculture: macadamia plantation

This study partly focussed on a macadamia plantation, which is under intensive irrigation and fertilization and other agricultural management practices. This plantation had the highest overall carabid abundance and species richness (S^*) of the eight sites studied. It was dominated by three species out of thirteen recorded. These three undescribed species from the Harpalini tribe (Harpalini sp. 126, 115b, 150) comprised 94% of the total catch. In addition, other species, such

as *Hyparpalus tomentosus* and the Pterostichini species *Metagonum gilvipes*, were all observed in heaps of leaf litter on the ground. The rare species, unique to this site, were Chlaeniini species (*Chlaeniostenus cylindricus* and *Chlaenius vitticolis*); Lebiini species (*Poecilothais tetragramma* and *Pentagonica gracilis*) and undescribed Carabidae sp. (276).

One factor responsible for the high abundance at this site is likely to be intensive irrigation which provided a constant high soil moisture. Additionally, the heaps of leaf litter provided shelter and prey. This macadamia habitat therefore has major implications for conservation of biodiversity. Islands of heaps of leaf litter should be incorporated into the management of macadamia plantations, and possibly other types of plantation crops, for enhancing biodiversity. Possibly also, these carabids are playing an important role in maintaining pest levels below economic threshold, especially as these macadamias did not need any major pest control measures. Further research however, is needed to determine whether these carabid species are indeed effective as natural enemies of macadamia pests. It is clear that biodiversity can be enhanced in agroecosystems as well as nature reserves (Fry, 1989; Fry and Lonsdale, 1991).

Carabids are common in agricultural fields in the northern hemisphere. Agriculture profoundly influences the composition, abundance, and spatial distribution of ground beetles through the use of agrochemicals, changes in habitat structure from cultivation methods and crop type (Desender *et al.*, 1994; Stork, 1990; Luff, 1987; Thiele, 1977). Since an early publication by Forbes, (1883), carabids have generally been considered beneficial natural enemies of agricultural pests (Thiele, 1977; Allen, 1979), although a few species are pests themselves (Luff, 1987; Thiele, 1977).

The carabid fauna of agricultural fields originated in riparian (Thiele, 1977) or steppe habitats (Lovei and Sarospataki, 1990). Data are few outside Europe and North America. In Canada, many species in cultivated land are either introduced European species (Allen, 1979; Spence and Spence, 1988) or North American representatives of genera common in European agricultural fields, such as *Pterostichus*, *Harpalus*, or *Agonium*. In Japan, the fauna is similar to that of the European cultivated habitats at the generic level (Luff, 1987), although species of *Chlaenius* and *Carabus* can be abundant (Yano *et al.*, 1989). In arid areas, Tenebrionidae are more prevalent than Carabidae (Fragalla and Adam, 1985). In New Zealand, carabids can be significant predators (Barker, 1991), but they are not as prevalent there as they are in northern hemisphere

cultivated fields (Lovei, 1991).

This study has shown the prevalence of Carabidae (especially within the Harpalini tribe) in an agricultural setting in southern Africa. It is not possible at present to compare the genera and species within this tribe, as well as many other tribes, with those in the northern hemisphere, due to the taxonomic impediment, especially within the Harpalini in South Africa.

6.3 THE NEED FOR INTEGRATED MANAGEMENT

Ecological knowledge is imperative when modifying the present harvesting methods in forestry management to minimize their harmful effects on biological diversity (Niemela, 1997). However, the type of information provided by scientists is not always relevant to managers. Consequently, improved collaboration among all parties involved is necessary. This way, the requirement of nature protection and development or resource harvesting can be considered simultaneously to develop socio-economically acceptable and ecologically sound policies. To achieve this goal, Haila (1994) and Franklin (1995) proposed integrating science, management, and policy according to the following sequence: (1) develop new ecological knowledge through scientific research; (2) use this knowledge to alter management practice; (3) validate the new practices (4) implement the new practices. Usually management changes rarely follow this sequence. Often other objectives drive decisions, with scientific knowledge not being integrated into management practices. An example is the rapid paradigm shift concerning the management of Fennoscandian boreal forest. Strong public pressure to change the way forestry has been practised surfaced so rapidly that research was not able to keep pace. More recently considerable new knowledge relevant to management of boreal forests has been generated (Niemela, 1997). Results of this research have been used to alter management practices, and the new practices are increasingly being subjected to experimental validation and consequent adjustments.

Heterogeneity on all ecological scales is the rule in all natural ecosystems. Furthermore, because species richness of different taxa do not correlate well (Niemela *et al.*, 1996; Lawton *et al.*, 1998), conservation of total biodiversity is not possible (Usher, 1992). This variability in composition of species assemblages and in local environmental conditions underlies the necessity to think globally and act locally. Conservation strategies must be adapted to local conditions, combined with flexibility and the adjustment of methods to maximize biodiversity

conservation.

CHAPTER 7

CONCLUSIONS

1) SAMPLING METHODS

Thirty seven species from nine tribes and nine subfamilies were collected over the whole sampling period. A total of 4201 individuals in 35 species were collected by the three trap sampling methods (pitfall traps: $n=4197$; glass window traps: $n=4$ (in two species *Dromica gilvipes* and *Cicindela marginella inanis* which were also collected in pitfall traps); PVC-netting window traps: $n=0$). The visual or hand searching method produced 254 individuals in 19 species, of which 17 species were also caught in the pitfall traps and the other two individuals in two species (*Craspidophorus impictus* and *Chlaenius fasciger*) were caught neither in pitfall traps or in any other trap. The percentage proportions collected by visual searching relative to pitfall trapping in terms of number of individuals was 6% and in terms of species 51%. Out of the thirty seven species collected over the whole study area, only four were cicindelids and the rest were carabids. In addition, eleven species out of the total thirty seven collected were undescribed.

The collecting method of pitfall trapping was found to be the best when compared to window trapping and visual searching methods. Far more individuals and species were caught by the pitfall trapping method. Although the relative merits and disadvantages of pitfall trapping are well known, pitfall catches in this study provided adequate numbers of individuals on which statistical analysis could be carried out and meaningful conclusions drawn. However, it was noted that it is important to tailor a sampling programme to the species and habitats with which one works and interpret the data obtained from a sounder base of biological intuition. The choice of a sampling method depends on the questions to be studied. In surveys of large geographical areas where the objective is qualitative inventory and comparison of assemblages, pitfall trapping is the only realistic alternative presently available.

The numbers of species and individuals caught in forest and grassland habitats in this study can

be said to be species-rich communities, as is the case in the northern hemisphere. In terms of species composition, there is a taxonomic impediment in the southern African species, particularly Harpalinae. However, the patterns, in terms of species and numbers caught in different habitats, is generally similar.

Although pitfall sampling carried out during one year, or at least the whole activity season of the species, gives a reliable estimate of the densities of active adult specimens, sampling over two seasons makes it much easier to interpret data.

2) SPECIES CUMULATIVE CURVES

Results of cumulative species curves over the two years sampling seasons and the presence of many large species appear to suggest that these species are characterized by relatively long adult life-span, which may enable them to be used in short-term carabid sampling (spring sampling, summer sampling, autumn sampling) for site assessment studies.

3) SEASONAL POPULATION VARIATION

Seasonal rhythms with dormant periods during winter and/or summer are an integral part of the life history of temperate-region ground beetles. This is also the case for carabids of this region. The seasonal population variations in these landscapes appear to be at least partly habitat-specific and are affected by the intensity and type of disturbance, seasonal climatic changes from one year to the next and adjacent habitats. An intensively mown lawn in a park had the highest population variation and was a sink habitat.

Dufrene *et al.* (1990) used correspondence analysis (CA) to compare the temporal distribution of carabid communities in two different regions in Belgium. The same technique was used here, but using PCA instead of CA, and has shown that PCA gives a better visual impression of the actual species abundance relative to each other and to the sampling period (month) using the species oblique axis. It is also a quick and easy way of comparing activity patterns such as timing of occurrence and abundance of individual species in many habitats.

4) SPECIES DIVERSITY

Trends in the response of species to various landscape disturbances reported in studies in the northern hemisphere were similar to those found in this study. In grasslands, anthropogenic disturbance increased species richness more so by fire than by cutting. However, intensive disturbance results in sink habitats as in the park. In forests, disturbance decreased species richness but increased abundances. The most species-rich habitats were those with intermediate disturbance.

The theoretical number of species (S^*) from the lognormal model was found to be a more reliable measure of species richness when comparing different habitats. In forest habitats, a macadamia plantation was the most species-rich, and the pine plantation the least species rich. Grasslands with fire management were more species-rich than those that were cut.

Distribution of species in habitats relative to disturbance showed that mean body size of assemblages decreased with disturbance: disturbed forests (pine and macadamia plantations) had fewer rare species and more common ones, while natural forests (indigenous forest and *Acacia*-woodland) had more rare species. Grasslands with fire had more rare species than common ones. Grasslands that were frequently mown (parks) had few rare species and very few common ones. Grasslands that were mown infrequently (hayfields) had more common species than frequently mown ones. The same pattern of higher numbers of rare species in grasslands as compared with forests has been documented in the northern hemisphere.

The use of graphical distributional $\times 2$ geometric plots agreed with studies in the northern hemisphere in that species falling in the intermediate abundance classes 3 - 5 are the most sensitive to disturbance and can be used in monitoring programmes as bioindicators. In the northern hemisphere, this method has been used to monitor pollution in aquatic systems. It was applied here successfully. The suggestion that intermediately abundant species could be used as indicators can be operationalised in a management scheme by initially identifying the group and then focussing on that group of species which would then be subjected to further monitoring, rather than monitoring a whole range of species.

The mystery of the 'missing species' reported by Niemela (1993) is not only peculiar in the boreal environment but also in forests in the southern hemisphere, although further data are

required to increase sample size for a better comparison. However, in the southern hemisphere, species are probably also regulated by availability of food, competition and the physical environment.

5 SPECIES -ENVIRONMENT RELATIONSHIPS

Ordinations led to the recognition of six ecologically-meaningful habitat groups:

- I) adjacent mistbelt natural indigenous forest and pine plantation. Natural forest was found to be a source habitat and pine forest may be a sink habitat but this is uncertain since population dynamics, reproduction and movement between habitats were not studied.
- II) recreational park grassland (may be a sink habitat).
- III) sandy road verge grassland (high conservation value).
- IV) macadamia plantation (most species-rich).
- V) *Acacia*- woodland
- VI) road verge with adjacent hayfield

This study showed that soil characteristics namely, pH, moist soil/sand and twig and/or leaf litter determine carabid and cicindelid species occurrence. Land-use and management regimes influence these patterns. The effect of altitude is masked by the presence of soil characteristics in a multivariate analysis, and more so in the presence of pH and moist soil/sand gradients from one altitude to the next. In the absence of soil characteristics, or in a univariate analysis, the altitude factor then appears to be very important. Altitude has therefore an indirect effect on species occurrence in that it determines climate, which in turn, determines soil types and vegetation types.

6) MANAGEMENT RECOMMENDATIONS

- I) Do not remove branches after pruning in forest habitats.
- II) Do not mow but burn road-side verges (good for rare species).

III) In recreational parks, stones, leaf litter and shade should be maximized.

IV) Undertake rotational burning and or cutting in parks and hayfields.

V) Maximize microhabitats (i.e. habitat heterogeneity).

7) MACROECOLOGY

A macroecological approach was successfully applied in this study and has shown that patterns and responses of ground beetles to various landscape disturbances is applicable both in the northern and southern hemispheres, with distinct similarities but occasional, local differences.

This study has also shown, among other things that, pitfall captures of carabids and cicindelids can be used to characterize various landscape types and disturbances at the landscape level and at point habitats within landscapes; pitfall captures of these animals can be used to monitor and evaluate temporal changes in habitats; species that can, and those that cannot, survive particular disturbances, especially in grasslands of sandy road verges have been identified and species assemblage distributions have been used for making management recommendations to improve the conservation of landscapes.

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(Table 4.26 Appendix 2).

In the top left-hand side of the diagram (Fig. 4.28), are point habitats belonging to the sites situated in the low altitudes of the savanna zone being S5 (17-20); S6 (21-24); S7 (25-28); S8 (29-32), which are more similar to each other just as was observed at the landscape level (Fig. 4.17). Specifically, at S5 and S6, Carabidae sp. (023) was recorded in all point habitats but reached abundance in point habitat 18 and 20 at S5 and point habitat 23 and 24 at S6 with an overall higher abundance at S5. The species *H. mniszechi* (024) was recorded in all point habitats at S5, except point habitat number 19. Species *L. immaculata* (034), *P. bipustulatus* (029), Harpalini sp. (030) were only recorded in some of the point-habitats at S5, (Table 4.26 Appendix 2).

In the point habitats of S7(25-28) and S8(29-32), the Harpalini sp. (008), Harpalini sp. (017), although eurytopic, reached maximum abundance at S7 at point habitat number 27. Harpalini sp. (017) was recorded in all point habitats at S5 and S8 with maximum abundance in S7 at point habitat 26. Harpalini sp. (020) was recorded in all point habitats at S7 with maximum abundance at point habitat number 26. The other species, Harpalini sp. (035), *C. vitticolis* (027), *P. gracilis* (025), *C. cylindricus* (021) were recorded only in some of the point habitats at S7 (Table 4.26 Appendix 2).

In the centre of the diagram (Fig. 4.28), are species *M. gilvipes* (001), Harpalini sp. (009), *H. atratus* (007), which are eurytopic to sites both at high and low altitude, but reached maximum abundance in sites (S1, S2, and S3), at high altitude (Table 4.26 Appendix 2). Species *D. gilvipes* (015) and *C. caffer* (012) were eurytopic to sites S4, S5 and S6. *D. gilvipes* (015) was present in all point habitats at S4 and S6 and in only one point habitat number 18 at S5 which was situated nearer to S6.

In the bottom-left hand of the diagram, (Fig. 4.28), are point habitats (13-16) belonging to S4. Species *E. caffer* (033) was recorded in all point-habitats. Species *D. carinulata* (018), *C. inanis* (019) and *G. subhamatus* (014) were recorded in all point habitats with maximum abundance in point habitat number 13. Cicindelini sp. (016) was only recorded at point habitat 13; *P. simplex* (022) at point habitat number 15 and *M. atriceps* (013) at point habitat number 16.

4.7.2.2.2 PCA at the point habitat level using species data of the first sampling season

When CA was carried out, the ordination diagram produced had all the sites and species points of all the sites situated at the centre of the diagram making it impossible to interpret the ordination. The same thing happened with the same data in MDS analysis with the PRIMER program (Fig. 4.12b). Next, DCA was carried out and the resulting ordination diagram had all species and site points situated in a perpendicular position to the first axis at 1.5 units starting with sites at high altitude and ending with those at lower altitude. Again it was not easy to interpret this diagram. The results of both CA and DCA were found to be less than 1.5 standard deviations and it was therefore safe to use PCA (Ter Braak, 1988).

Fig. 4.29 is the PCA ordination diagram produced which has the species and site points placed in positions similar to those of CA at the landscape level, (Fig. 4.24). The eigenvalue of the first axis ($\lambda_1=0.583$) and the second axis was ($\lambda_2=0.108$) with 69% cumulative variance of species data.

The species, *Lebiini* sp. (032), *Abacetus* sp. (213), *C. pseudocastellani* (038), *Harpalini* sp. (35a), *S. alternaris* (254), *S. fenestratus* (45a), *M. nanum* (140), were recorded in point-habitats (1-12) of S1, S2 and S3. The *Lebiini* sp. (032) was recorded in all point-habitats of S1 and S2 but reached maximum abundance in point habitat numbers (5, 6, 8) of S2. At S3, this *Lebiini* sp. (032) was recorded in some of the point-habitats (8, 12). The *Abacetus* sp. (213) was recorded in some of the point habitats at S1 and S2, but reached maximum abundance in point habitats at S2.

The *Harpalini* sp. (35a) was eurytopic to S2, S5 and S6 with maximum abundance in S2. *S. alternaris* (254) was recorded in some of the point habitats at S1 and S3. Species *S. fenestratus* (45a) and *M. nanum* (140) were recorded at point habitat numbers 10 and 11 of S3 respectively.

Site 4 with point habitat numbers (13-16), species recorded were *C. inanis* (007), *D. carinulata* (014), *D. gilvipes* (250a). The point habitats were not marked on the diagram (Fig. 4.29) because they were too close to each other, meaning that they are very similar to each other as they share many species. At S5, *Carabidae* sp. (243) was recorded in all point habitats and in some of the point habitats at S6 and S8. Species *H. mniszehi* (105) was recorded in all point habitats at S5, except point habitat number 19.

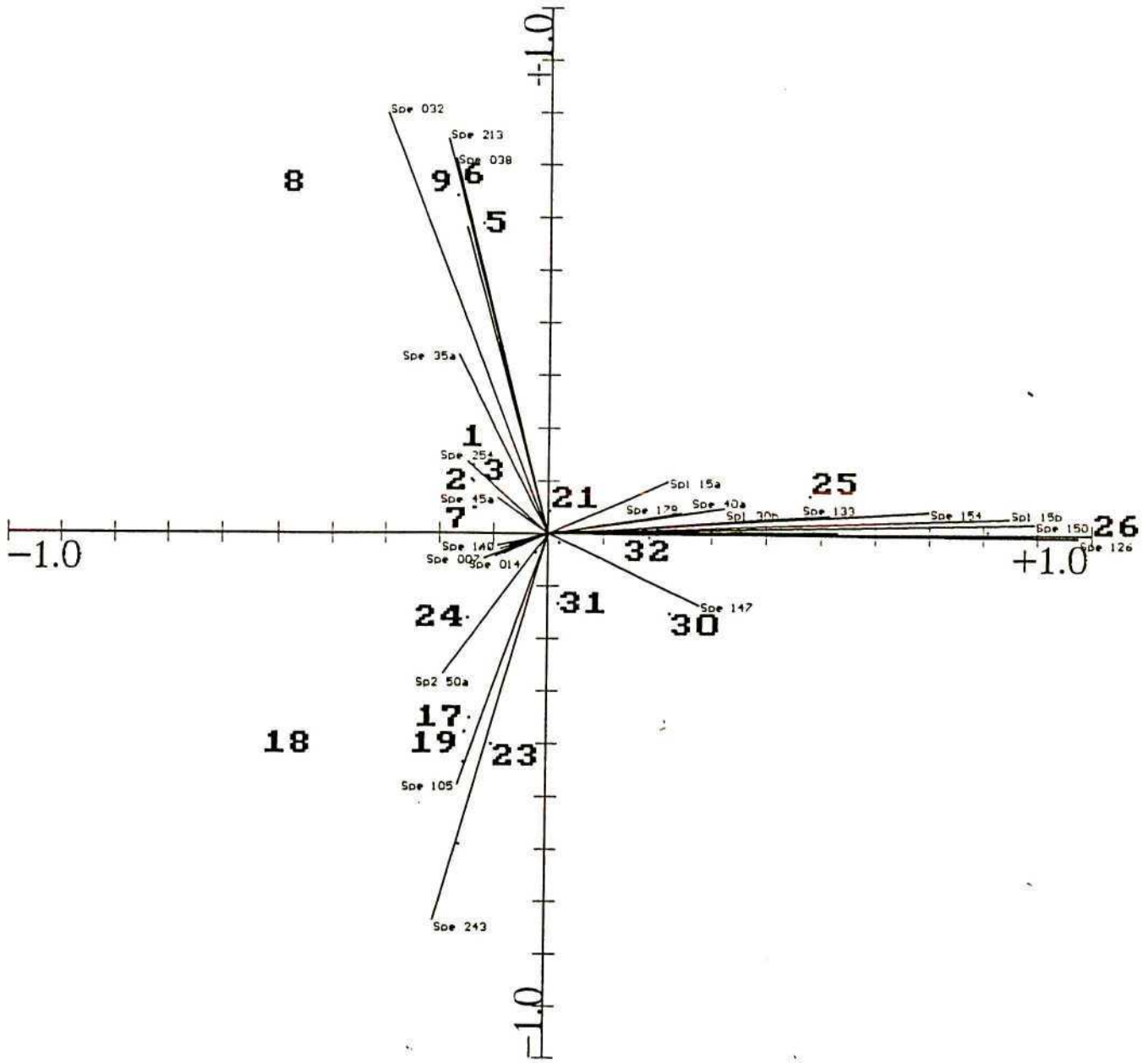


Figure 4.29: Ordination diagram of principal components analysis (PCA) of carabid and cicindelid species data at the point habitat level, using data over the first sampling season, June 1994-May 1995, (Table 4.24). The first axis $\lambda_1=0.583$ is horizontal and the second axis $\lambda_2=0.108$ is vertical. The diagram shows the distribution of species among the 32 point habitats of the eight sites. Species are shown by oblique axis in small type numbers, using code numbers listed in Table 4.24. CANOCO was used.

In the right-hand side of the ordination diagram (Fig. 4.29), are point habitats belonging to S7 and S8 (25-32). Harpalini sp. (126), Harpalini sp. (115b) were recorded in all point habitats at S7 and S8 with maximum abundance in point habitat 26. The species *C. vitticolis* (154), *H. tomentosus* (133), *P. gracilis* (130b), *C. cylindricus* (40a) and *C. caffer* (178) were recorded in lower abundance in some of these point habitats (Table 4.24 Appendix 2). Species *M. gilvipes* (115a) was eurytopic to many sites (S1, S2, S3, S4, S5, S8) but had maximum abundance at S7 in point habitat 25. Species *H. atratus* (147) was recorded in forest sites in some of the point habitats (S1, S5 and S7). These inferences agree with observed data in Table 4.24 Appendix 2.

4.7.2.2.3 CA at the point habitat level using species data of the second sampling season

Fig. 4.30 is the ordination diagram resulting from this analysis. The eigenvalue of the first axis ($\lambda_1=0.823$) and the second axis is ($\lambda_2=0.788$) with 29.4% cumulative variance of species data. The placement of sites, point-habitats and species in this ordination diagram was similar to that at the landscape level (Fig. 4.26).

In the top-left hand side of the diagram, (Fig. 4.30), are point habitat numbers (13-16) in S4. The species *D. gilvipes* (250a) was only recorded at point habitat 13. Species *G. subhamatus* (240a) was only recorded at point habitat 13 and 14 with maximum abundance at point habitat 13. Point-habitat 13 was situated in an area where the disturbance of cutting grass was carried out. It appears that these two species thus prefer more open habitats. Species *E. caffer* (115a-w), was recorded in all the point habitats only in the second sampling season and none in the first sampling season. The species *M. atriceps* (181) was only recorded at point habitat number 16.

In the lower left-hand bottom corner of the diagram (Fig. 4.30), are point-habitats belonging to S2, S1 and S3 (1-12). *Abacetus* sp. (213) was in all point habitats at S1 and S3. *C. pseudocastellani* (038), *Lebiini* sp. (032) was in all point habitats at S1 and S2. *M. nanum* (140) and *H. atratus* (147) were in some of the point habitats at S1, S2 and S3. *S. alternaris* (254) was at point habitat number 1 at S1. The Harpalini sp. (35a) was eurytopic but reached maximum abundance at S8 point habitat number 29. The other eurytopic species were *M. gilvipes* (115a) and *L. insidiosa* (130a). Species *M. gilvipes* (115a) was eurytopic in point habitats of S1, S2, S3, S4 and S5 but reached maximum

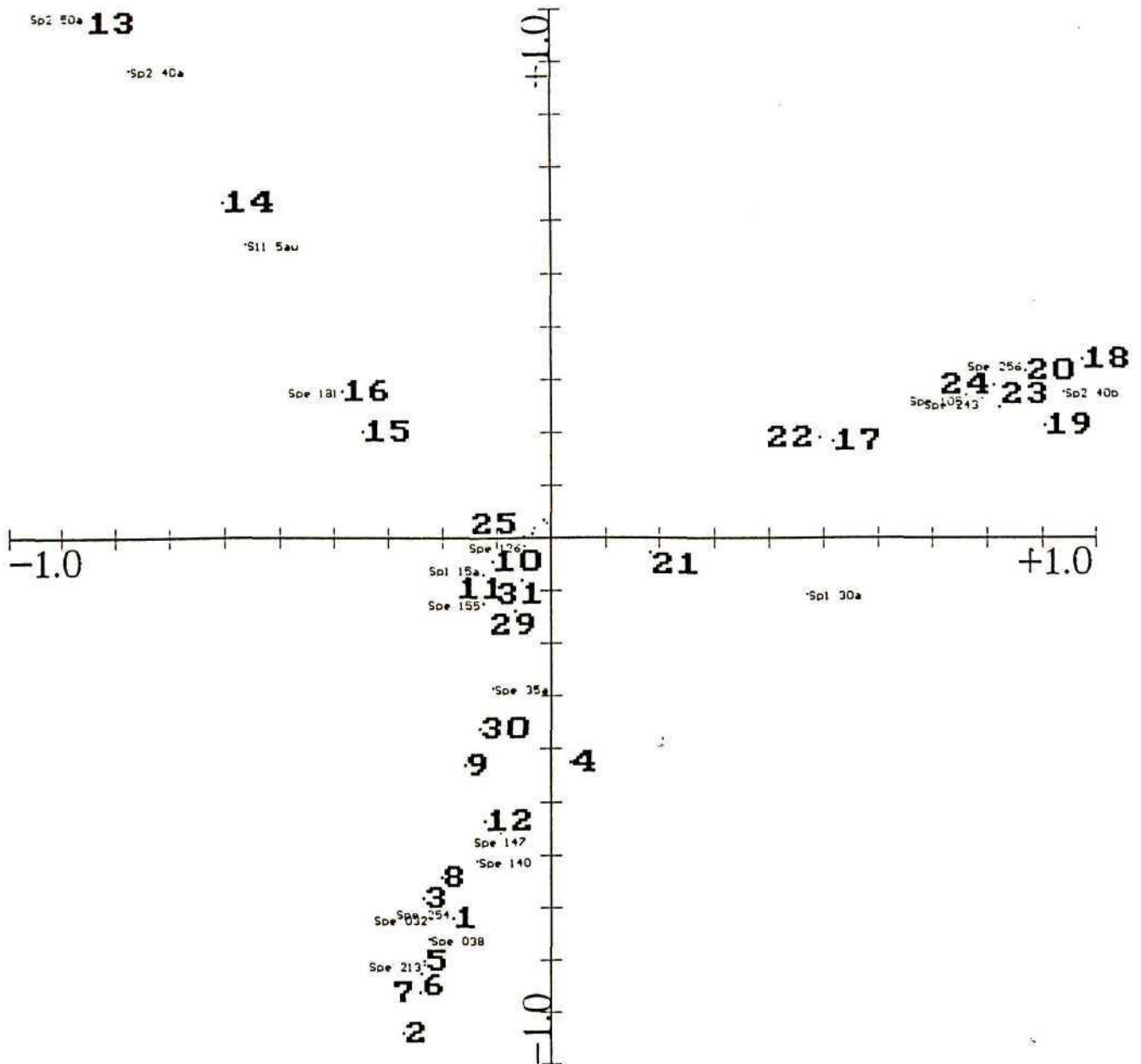


Figure 4.30: Ordination diagram of correspondence analysis (CA) of carabid and cicindelid species data at the point habitat level, using data over second sampling season, June 1995-May 1996, (Table 4.25). The first axis $\lambda_1=0.823$ is horizontal and the second axis $\lambda_2=0.788$ is vertical. The diagram shows the distribution of species among the 32 point habitats of the eight sites. Species are shown as code numbers in small type following the order of listing in Table 4.25. CANOCO was used.

abundance at point habitat number 11 of S3 and point habitat 16 of S4, both grasslands at high altitude. Species *L. insidiosa* (130a) was recorded in the natural forests at high and low altitude, being S5 (point habitat 19) and S1 (point habitat 4).

In the centre of the diagram (Fig. 4.30), are point-habitats belonging to S7(25-28) and S8(29-32) which have not been recorded in the diagram due to space. The dots at the centre next to point habitat 25 represents, Harpalini sp. (115b), Harpalini sp. (126) and Harpalini sp. (150) in addition to Harpalini sp. (126) that reached maximum abundance at S7.

In the left-hand side of the diagram (Fig. 4.30), are point-habitats belonging to S5(17-20) and S6 (21-24). The Carabidae sp. (243) was recorded in all point-habitats at S5 and S6 with overall dominance at S6. The species *H. mniszewski* (105) was recorded in all point habitats at S5 except point habitat number 19. The Cicindelidae sp. (240b) was recorded at S5 at point habitat 15 and 19.

4.7.2.2.4 Species spatial patterns in road verge grasslands using CA

In Fig. 4.29, patterns of point habitats belonging to S4(13-16) were not shown as they were situated close to the centre of the diagram. In order to get a better view of the placement of these point habitats relative to each other in an ordination diagram, CA of S4 and S6 alone was carried out for the first and second sampling seasons as seen in Fig. 4.31 and Fig. 4.32 respectively.

The type of landscape disturbance at these sites was autumn burning of grass along the road verges as a city management strategy of preventing accidental fires in addition to the prevention of bush encroachment. In the first sampling season (June 1994-May 1995) both sites received autumn burning beginning of June. But at S6, point habitat numbers 21 and 22 did not receive fire (i.e. they remained as islands of unburnt grass) and point habitats numbers 23 and 24 burnt completely. Therefore, the intensity of the disturbance burning was relatively higher at S4 than it was at S6 during the first sampling season. In the second sampling season (June 1995-May 1996) autumn burning took place at S6 but the area in which the four point habitats (21, 22, 23, 24) were situated did not receive any burning. At S4, autumn burning did not take place but the area occupied by point habitat number 13 received the disturbance of cutting grass in five metres wide and along the electricity posts.

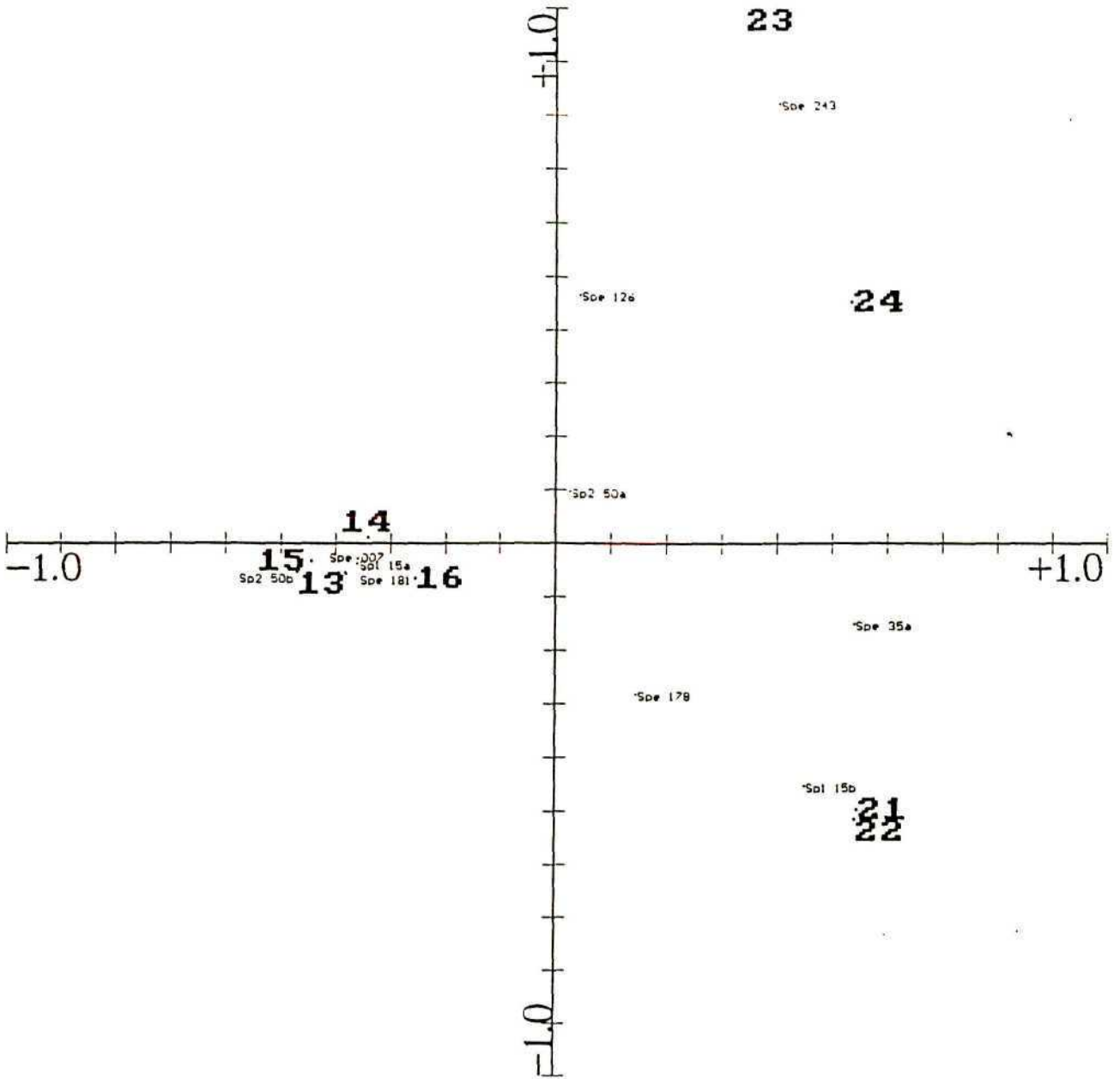


Figure 4.31: Ordination diagram of correspondence analysis (CA) at the point habitat level of two grassland road verges (as S4, with point habitats 13-14 and S6, with point habitats 21-24 shown in bold type numbers), using carabid and cicindelid species data over the first sampling season, June 1994-May 1995, (Table 4.24). The diagram shows the distribution of species among the eight point habitats of the two sites. Species are shown as code numbers in small type following the order of listing in Table 4.24.

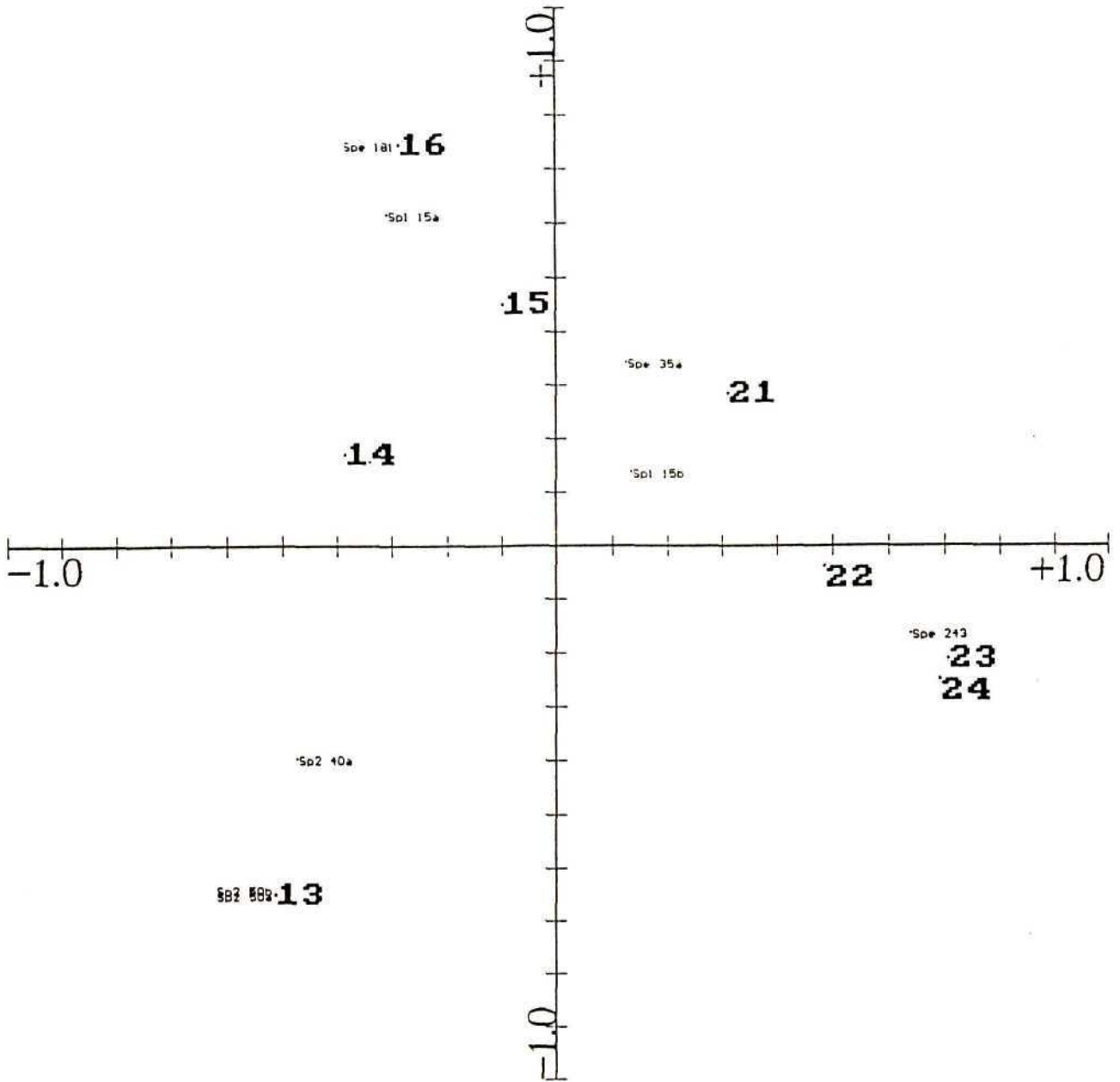


Figure 4.32: Ordination diagram of correspondence analysis (CA) at the point habitat level of two grassland road verges (as S4, with point habitats 13-14 and S6, with point habitats 21-24 shown in bold type numbers), using carabid and cicindelid species data over the second sampling season, June 1995-May 1996, (Table 4.25). The diagram shows the distribution of species among the eight point habitats of the two sites. Species are shown as code numbers in small type following the order of listing in Table 4.25.

In the left-hand side of the diagrams (Fig. 4.31 and Fig. 4.32) are point habitats at S4 (13-16). In the first sampling season (Fig. 4.31) these point habitats shared many species and are therefore placed very close together. The area having been burnt completely, colonization took place during this year. Species that were recorded in all point habitats at S4 are *D. gilvipes* (250a), *M. gilvipes* (115a), and *C. inanis* (007). The others namely, Cicindelidae sp (250b), *Pachydinodes simplex* (40b), *Graphipterus subhamatus* (240a), *Dromica carinulata* (014), Harpalini sp. (150), and *Metaxymorphus atriceps* (181) were only recorded in some of the point habitats (Table 4.24 Appendix 2).

In the centre of the diagram (Fig. 4.31), *Metagonum gilvipes* (115a), *Dromica gilvipes* (250a), *Callistomimus caffer* (178), and Harpalini sp. (126) were eurytopic to both sites at S4 and S6.

In the right hand of the diagram (Fig. 4.31), Carabidae sp. (243) and Harpalini sp. (35a) were exclusively recorded at S6.

During the second sampling season Fig. 4.32, the area covering point habitat number 13 received the disturbance of cutting grass, the rest of the habitats had tall grass throughout the season. This created a different microhabitat for species at point habitat number 13. The species that were only recorded at this point only were, Cicindelidae sp. (240b), *C. icindela inanis* (007), *Dromica gilvipes* (250a). The Carabidae species *Euleptus caffer* (115a-w) which had not been recorded in the first sampling season appeared in all the point habitats at S4.

Species shared between the two sites (S4 & S6) were Harpalini sp. (35a) and Harpalini sp. (115b). The point habitats at S6(21-24) appeared more similar in the second sampling season than those in the first.

4.8 DIFFERENCES IN THE APPLICATION OF CANOCO AND PRIMER

In community ecology, Ludwig and Reynolds (1988), have recommended the use of more than one method on a data set to confirm results. PRIMER and CANOCO computer softwares tackle essentially similar problems, though using different techniques. The use of the two ordination methods, MDS using PRIMER and CA/CCA using CANOCO, were carried out to detect any

variability in the results produced and therefore determine the appropriate method for the data, and also to gain experience in the use and application of both methods and the computer softwares.

The two methods produced ordination diagrams that separated the eight sites in a similar manner and isolated the same most important environmental variables responsible for the observed species patterns. The only difference was in ordering the most important soil characteristics. In order of importance, PRIMER listed them as pH, sand, litter and moisture, and CANOCO listed them as pH, litter, moisture and sand.

CANOCO has the option of presenting site points, species points and environmental variables in one ordination diagram therefore making it possible to see the distribution of species among sites along environmental gradients in one ordination diagram. PRIMER does not have this option but it can superimpose each environmental variable on each site point in as many diagrams as there are variables. CANOCO also has this option too. PRIMER does not present species in the ordination diagram but through the program SIMPER it gives a print out of the discriminator species that are responsible for the creation of various clusters or groups produced by ordination or cluster analysis.

To test for significant differences between groups, PRIMER does this through analysis of similarities and CANOCO uses Monte Carlo permutation tests.

CANOCO gives several options of ordination methods namely, principal components analysis (PCA) and redundancy analysis (RDA); correspondence analysis (CA) and canonical correspondence analysis (CCA); detrended correspondence analysis (DCA) and detrended canonical correspondence analysis (DCCA) in addition to hybrid options that one can choose from in case one needs to try out with several methods before arriving at one that best suits a particular data set. For example, in (Fig. 4.12 b), MDS was not able to separate the point habitats within the eight sites in one analysis neither could CA or DCA do this. However, separations were obtained in both methods by dropping some samples from the analysis. PCA was able to separate the various point habitats of the various sites in one analysis (Fig. 4.29) even though PCA is not recommended for species data in community ecology as it is not linear (Ter Braak, 1988), it worked well for this set of data. PRIMER only gives one ordination method NMDS and uses PCA for analysing environmental variables, but CANOCO

gives several ordination methods namely, PCA, RDA, CA, CCA, DCA, DCCA etc.

PRIMER can give species rank curves and geometric plots for sites and CANOCO does not have this facility.

PRIMER can carry out cluster analysis and produce dendrograms whereas CANOCO cannot.

In PRIMER, data formats can be done using common spreadsheets such as EXCEL, LOTUS 123 and QUATTRO PRO etc., and one can save graphics produced in the analysis as graphic metafiles (.cgm) and export from PRIMER to standard presentation graphic programs such as Harvard graphics, Novell perfect office presentations etc., for polishing. This is one area that makes PRIMER more user friendly than CANOCO. This facility is not available in the current 1994 CANOCO version. Both methods were adequate for my type of data and any of the two methods could have been used. Therefore, CANOCO or PRIMER can be used depending on how one wishes to present one's data.

4.9 MEAN BODY SIZE OF SPECIES ASSEMBLAGES

Table 4.36 illustrates, basic statistics of the mean body size of carabid and cicindelid species assemblages in each of the eight sites arranged in order of increasing body size which is also the order of increasing intensity of disturbance.

Road verge grasslands (S4 and S6) with autumn burning disturbance had species assemblages with the smallest mean body size (10.38 mm and 11.17 mm respectively). Next was the macadamia plantation under agricultural management (irrigation, pesticides, fertilizers) with a mean body size of 11.31 mm. At a recreational park (S3) with frequent mowing of lawn, the mean body size of the carabid assemblage was 11.33 mm. Species found in a pine plantation (S2) in the middle successional stage had a mean body size of 11.43 mm. While those found in a natural indigenous forest (S1) had a mean body size of 12.78 mm. Next is the species assemblages in a natural *Acacia*-dominated woodland (S5) with 13.40 mm. Finally, a field of hay (S8) with annual autumn cutting had species with the largest mean body size. The smallest species at (S8) was 6 mm and the largest species was 30 mm. *Craspidophorus impictus* was the overall largest carabid collected (30 mm).

Sites	Body size (mm) \bar{x}	Standard deviation	Minimum body size (mm)	Maximum body size (mm)	Number of species (n)
S4 road verge	10.38	4.03	6	20	14
S6 road verge	11.17	7.05	6	25	6
S7 macadamia	11.31	4.75	6	20	13
S3 park	11.33	3.61	6	16	10
S2 pines	11.43	2.99	7	15	8
S1 mistbelt forest	12.78	3.38	6	16	10
S5 <i>Acacia</i> woodland	13.40	6.72	4	25	11
S8 hayfield	16.83	9.60	6	30	5

Table 4.36: Basic statistics carried out using MINITAB-ANOVA, showing mean body size (\bar{x}) of carabid and cicindelid species assemblages in each of the eight sites (S1 - S8), arranged in order of increasing body size which is also the order of increasing intensity of disturbance. The mean values of body sizes are significantly different ($P=0.04$).

These results show that, the grassland sites with minimum cutting disturbance (a field of hay S8) i.e. once a year had the highest mean body size (16.83 mm) and grasslands with intensive autumn burning had the lowest mean body size.

In forest sites, an *Acacia*-dominated woodland under nature management had the highest mean body size (13.40 mm) and macadamia plantation (S7) with agricultural management had the least mean body size (11.31 mm). Therefore, body size appears to decrease with increasing intensity of disturbance. In addition, carabid assemblages in a natural indigenous forest (S1) and an adjacent pine plantation (S2) were similar, hence their closeness in mean body size values (12.78 mm and 11.43 mm respectively). However, the mean body size value in the pine plantation (S2) is still lower, therefore it appears that body size decreases with increasing disturbance. It can therefore be concluded that, the mean body size of carabid assemblages in forest and grassland sites decreases with increasing intensity of disturbance.

4.10 TAXONOMIC SUMMARY OF SPECIES

There was a total of 4197 individuals and 37 species belonging to nine different tribes (Table 4.1) recorded over two seasons.

Species from the Tribes Oodini, Axinidiini and Panagaeini were recorded in low abundances in sites at high altitude (S1, S3 only) (Tables 4.23, 4.26 Appendix 2). Specifically Oodini species *Systolocranius alternaris* (254) reached maximum abundance in the natural indigenous forest (S1), however in the Park (S3), it was recorded in the vicinity of trees (point habitat 12) providing twigs and litter for shelter. The Axinidiini species *Metaxinidium nanum* (140) which has been reported as rare in South Africa was recorded in forest and grassland sites (natural indigenous forest S1, pine plantation S2 and park S3). The Panagaeini species *Craspidophorus bonvouloiri* (252) was recorded in forest sites (S1 and S2) only.

Species of the Tribe Pterostichini and Lebiini were recorded in all sites except the savanna grasslands (road verge S6 and hay field S8). Specifically, Pterostichini species *Metagonum gilvipes*

(115a) was mainly recorded in forest sites both at high and low altitude (natural indigenous forest S1, pine plantation S2, *Acacia*-woodland S5, macadamia plantation S7). It was also recorded in grassland habitats (park S3 and road verge S4) but higher abundances were at point habitats that were near trees that provided shelter and leaf litter namely point habitat numbers 11 and 16 (Table 4.26 Appendix 2). The Pterostichini species *Cophosomorpha pseudocastellani* (38) and *Abacetus* sp. (213) appear to be forest species of the indigenous forest (S1) and the adjacent pine plantation (S2) with higher abundance in pine forest S2. The Pterostichini species *Euleptus caffer* (115a-w) was recorded at the road verge grassland S4 and was found abundant in the tall late successional grasses after autumn fire management. The undescribed Lebiini sp. (32) was recorded in forest and grassland sites (natural indigenous forest S1, pine plantation S2 and park S3) at high altitude with maximum abundance in pine plantation S2. In the grassland park S3, there was high abundance of these Lebiini sp. 32 in the vicinity of stones and trees. The Lebiini species *Hystrichopus atratus* (147) was abundant in forests under nature management both at high and low altitude (natural indigenous forest S1 and *Acacia*-woodland S5), it was also present in macadamia plantation. In grassland habitat (park S3), it was only found near trees. The Lebiini species exclusively common (i.e. not recorded in any other site) in forests under nature management both at high and low altitude (natural indigenous forest S1 and *Acacia*-woodland S5) was *Lebia nematopeza insidiosa* (130a). The Lebiini species *Hystrichopus mniszehi* (105) was only recorded in the savanna *Acacia*-dominated natural forest (S5).

Species of the Tribe Harpalini were recorded in all sites, but numbers of species and abundances increased highly in sites in the savannah grasslands and mainly in the macadamia plantation S7 e.g. Harpalini sp. (126), Harpalini sp. (115b), Harpalini sp. (150) see Table 4.23 Appendix 2.

Species of the Tribe Chlaeniini were recorded in low abundances in the macadamia plantation forest under agricultural management (S7), e.g. *Chlaeniostenus cylindricus* (40a), *Chlaenius vitticolis* (154), *Callistomimus caffer* (178), *Pachydinodes bipustulatus* (256).

From the Tribe Graphipterini, only one species *Graphipterus cordiger subhamatus* (240a) was recorded in the road verge grassland S4 with high abundance in the open patches and short grass.

From the Tribe Cicindelini, species were recorded only in the road verge grasslands (S4 and S6) with high abundance in the open patches and short grasses e.g. *Cicindela inanis* (7), *Dromica tuberculata carinulata* (14), *Dromica gilvipes* (250a), Cicindelidae sp. (250b).

From Tables 4.2-4.9 and 4.11-4.18 Appendix 2, the most dominant species in decreasing order in the indigenous forest (S1) at high altitude were: *M. gilvipes* (115a), *Lebiini* sp. (32), *C. pseudocastellani* (38). In the pine plantation (S2), they were: *C. pseudocastellani* (38), *Abacetus* sp. (213), *Lebiini* sp. (32), *Harpalini* sp. (35a). In the recreational park grassland (S3), there was just one species *M. gilvipes* (115a). In the road verge grassland at high altitude (S4), they were: *E. caffer* (115a-w), *M. gilvipes* (115a), *G. subhamatus* (240a), *C. inanis* (7).

In the *Acacia* savanna woodland (S5) they were: *Carabidae* sp. (243), *H. mnischechi* (105) and *M. gilvipes* (115a). In the road verge grassland (S6) at low altitude, they were, *Harpalini* sp. (115b), *Harpalini* sp. (35a). In a macadamia plantation (S7), *Harpalini* sp. (126), *Harpalini* sp. (115b), *Harpalini* sp. (150) and *M. gilvipes* (115a) were dominant. In a field of hay (S8), *Harpalini* sp. (115b), *Harpalini* sp. (126) and *Harpalini* sp. (35a) were dominant.

APPENDIX 1: TABLES IN CHAPTER 3

	JUNE	JULY	AUG	SEPT	OCT	NOV	DEC	JAN	FEB	MARCH	APRIL	MAY	TOTAL
94/5	21.1	20.8	22.3	26.2	22.6	26.0	28.4	27.6	30.0	25.6	23.0	22.6	296.2
95/6	21.1	20.8	24.3	26.2	23.8	24.9	24.0	26.0	26.8	25.5	23.0	22.6	289
AVE	21.1	20.8	23.3	26.2	23.2	25.5	26.2	26.8	28.4	25.6	23.0	22.6	292.7

(a)

	JUNE	JULY	AUG	SEPT	OCT	NOV	DEC	JAN	FEB	MARCH	APRIL	MAY	TOTAL
94/5	9.5	43.5	30.6	7.5	85.4	30.7	99.4	54.4	41.4	141.4	72.75	17.25	633.8
95/6	22.0	4.0	5.6	8.2	101.2	91.2	106.2	151	110	141.4	7.5	31.25	779.55
AVE	15.8	23.8	18.1	7.9	93.3	61	102.8	102.7	75.7	141.4	40.0	24.3	688.25

(b)

	JUNE	JULY	AUG	SEPT	OCT	NOV	DEC	JAN	FEB	MARCH	APRIL	MAY	TOTAL
94/5	71.1	67.6	86.0	85.1	96.5	93.3	95.7	96.6	94.1	97.4	98.5	96.0	1077.9
95/6	71.1	67.6	89.4	91.9	95.0	96.0	90.4	96.9	96.7	96.6	98.5	96.0	1086.1
AVE	71.1	67.6	87.7	88.5	95.8	94.7	93.1	96.8	95.4	97.0	98.5	96.0	1082.2

(c)

Table 3.3: Climate data for Savanna zone over the study period. (a) totals and averages for maximum temperature ($^{\circ}\text{C}$), (b) totals and averages for rain (mm), (c) totals and averages for maximum humidity (%).

	JUNE	JULY	AUG	SEPT	OCT	NOV	DEC	JAN	FEB	MARCH	APRIL	MAY	TOTAL
1994/5	18.8	19.1	20.4	24.4	21.2	25.2	26.5	26.1	28.5	23.8	21.0	20.3	275.3
1995/6	18.3	18.8	22.8	23.7	22.4	23.6	22.8	24.5	25.1	23.8	21.0	20.1	266.9
AVE	18.6	19.0	21.6	24.05	21.8	24.4	24.7	25.3	26.8	23.8	21.0	20.2	271.25

(a)

	JUNE	JULY	AUG	SEPT	OCT	NOV	DEC	JAN	FEB	MARCH	APRIL	MAY	TOTAL
1994/5	3.5	23.1	30.8	11.5	68.6	21.4	130.5	62.3	19.8	129.5	62.0	21.5	584.5
1995/6	29.8	2.5	9.8	19.8	95.1	110.1	303.6	147.0	169.8	140.3	17.5	89.4	1134.7
AVE	16.7	12.8	20.3	15.7	81.9	65.8	217.1	104.7	94.8	134.9	39.8	55.5	860

(b)

	JUNE	JULY	AUG	SEPT	OCT	NOV	DEC	JAN	FEB	MARCH	APRIL	MAY	TOTAL
1994/5	80.8	73.8	86.0	79.3	96.1	91.4	94.1	95.1	93.5	98.2	97.7	95.0	1081
1995/6	84.8	82.7	86.2	88.3	93.2	92.5	93.4	93.3	93.1	93.0	93.7	92.8	1087
AVE	82.8	78.3	86.1	83.8	94.7	92.0	93.8	94.2	93.3	95.6	95.7	93.9	1084.2

(c)

Table 3.4: Climate data for Escarpment zone over the study period. (a) totals and averages for maximum temperature (°C), (b) totals and averages for rain (mm), (c) totals and averages for maximum humidity (%).

APPENDIX 2: TABLES IN CHAPTER 4

	June	July	August	Sept	Oct	Nov	Dec	Jan	Feb	March	April	May	Total
Species	1 2 3 4	1 2 3 4	1 2 3 4	1 2 3 4	1 2 3 4	1 2 3 4	1 2 3 4	1 2 3 4	1 2 3 4	1 2 3 4	1 2 3 4	1 2 3 4	
115a	0 0 3 0				0 0 1 2 0	2 0 1 8 2	2 0 0 0						39
254						0 0 2 0	2 0 2 0						6
213								2 0 0 0	2 2 0 0				6
32			0 0 0 2	0 0 0 6		0 2 2 0						2 0 0 0	14
147										0 4 0 0			4
38							0 0 2 0						2
252						0 0 0 2							2
Tot. Abu	3	0	2	6	12	30	8	2	4	4	0	2	73
Cum. No.	1	1	2	2	2	4	5	6	6	7	7	7	7
Tot. No. Sp.	1	0	1	1	1	4	3	1	1	1	0	1	

Table 4.2: Number of individuals of carabid and cicindelid species as code numbers (see Table 4.1 for actual names) and cumulative number of species (Cum. No.), recorded for each monthly replicate over the first sampling season (June 1994 - May 1995), arranged for each of the four point habitats (1 2 3 4) at site 1. Blank cells indicate no species were recorded in the four point habitats. Total abundance (Tot. Abu.); Total number of species (Tot. No. Sp.).

	June	July	August	Sept	Oct	Nov	Dec	Jan	Feb	March	April	May	Total
Species	5 6 7 8	5 6 7 8	5 6 7 8	5 6 7 8	5 6 7 8	5 6 7 8	5 6 7 8	5 6 7 8	5 6 7 8	5 6 7 8	5 6 7 8	5 6 7 8	
32	0 3 3 0	4 0 0 0	0 0 0 2	0 4 0 0	1 4 4 0 8			0 6 0 4	0 0 0 2	0 2 0 0			56
115a			2 0 0 0		2 0 0 0	2 0 0 0							6
213			2 0 0 2			1 0 1 2 0 6	2 6 0 0	6 4 0 2	1 4 8 0 0	4 0 0 0	2 0 0 0		80
252					2 0 0 0			0 2 0 0	0 2 0 0				6
38						0 2 0 4	0 0 0 4	2 6 0 2	0 6 0 1 2	0 6 0 0	0 2 0 8	0 2 0 2	58
115b				2 0 0 0						0 2 0 0			4
150										0 0 0 1 8	0 0 0 6	0 2 0 4	30
Tot. Abu	6	4	8	4	32	36	12	34	44	32	18	10	240
Cu. No.	1	1	3	3	5	6	6	6	6	7	7	7	7
Tot. No. Sp.	1	1	3	1	4	3	2	4	4	5	3	2	

Table 4.3: Number of individuals of carabid and cicindelid species as code numbers (see Table 4.1 for actual names) and cumulative number of species (Cum. No.), recorded for each monthly replicate over the first sampling season (June 1994 - May 1995), arranged for each of the four point habitats (5 6 7 8) at site 2. Blank cells indicate no species were recorded in the four point habitats. Total abundance (Tot. Abu.); Total number of species (Tot. No. Sp.).

	June	July	August	Sept	Oct	Nov	Dec	Jan	Feb	March	April	May	Total
Species	9 10 11 12	9 10 11 12	9 10 11 12	9 10 11 12	9 10 11 12	9 10 11 12	9 10 11 12	9 10 11 12	9 10 11 12	9 10 11 12	9 10 11 12	9 10 11 12	
150						0 2 0 0			0 2 0 0				4
32				0 0 0 2		0 6 0 0			0 2 0 0				10
140										0 0 2 0			2
254					0 0 0 2								2
115a									0 0 0 2				2
Tot. Abu	0	0	0	2	2	8	0	0	6	2	0	0	20
Cu No.	0	0	0	1	2	3	3	3	4	5	5	5	5
Tot. No. Sp.	0	0	0	1	1	2	0	0	3	1	0	0	

Table 4.4: Number of individuals of carabid and cicindelid species as code numbers (see Table 4.1 for actual names) and cumulative number of species (Cum. No.), recorded for each monthly replicate over the first sampling season (June 1994 - May 1995), arranged for each of the four point habitats (9 10 11 12) at site 3. Blank cells indicate no species were recorded in the four point habitats. Total abundance (Tot. Abu.); Total number of species (Tot. No. Sp.).

	June	July	August	Sept	Oct	Nov	Dec	Jan	Feb	March	April	May	Total
Species	13 14 15 16	13 14 15 16	13 14 15 16	13 14 15 16	13 14 15 16	13 14 15 16	13 14 15 16	13 14 15 16	13 14 15 16	13 14 15 16	13 14 15 16	13 14 15 16	
240a				2 0 0 2								2 0 0 0	6
14						8 0 2 8	2 0 0 0						20
7						4 2 2 8	0 2 0 0						18
250a					0 6 2 6	2 0 0 0							16
250b						2 0 0 0							2
115a						0 0 2 0	0 0 2 2		0 0 0 6	2 1 2 2 0		0 0 0 2	30
150						0 0 2 2							4
40b							0 0 2 0						2
178		0 0 0 2											2
181		0 0 0 2											2
126					0 0 0 2								2
115b									0 0 0 2				2
Tot. Abu	0	4	0	4	16	44	10	0	8	16	0	4	106
Cu No.	0	2	2	3	5	10	11	11	12	12	12	12	12
Tot. No. Sp.	0	2	0	1	2	6	4	0	2	1	0	2	

Table 4.5: Number of individuals of carabid and cicindelid species as code numbers (see Table 4.1 for actual names) and cumulative number of species (Cum. No.), recorded for each monthly replicate over the first sampling season (June 1994 - May 1995), arranged for each of the four point habitats (13 14 15 16) at site 4. Blank cells indicate no species were recorded in the four point habitats. Total abundance (Tot. Abu.); Total number of species (Tot. No. Sp.).

	June	July	August	Sept	Oct	Nov	Dec	Jan	Feb	March	April	May	Total
Species	17 18 19 20	17 18 19 20	17 18 19 20	17 18 19 20	17 18 19 20	17 18 19 10	17 18 19 20	17 18 19 20	17 18 19 20	17 18 19 20	17 18 19 20	17 18 19 20	
243					4 6 26 0	8 8 0 0	4 6 8 52	0 0 2 4	0 2 0 0	0 4 0 0			134
115a							2 0 0 0	2 0 0 0	0 2 0 0	0 2 0 0	2 0 0 0		10
105							0 0 0 2		6 0 0 0	6 0 2 2	4 0 0 2	0 0 0 2	26
250a							0 2 0 0						2
35a												0 2 0 0	2
147												0 0 0 2	2
Tot. Abu	0	0	0	0	36	16	76	8	10	16	8	6	176
Cu No.	0	0	0	0	1	1	4	4	4	4	4	6	6
Tot. No. Sp.	0	0	0	0	1	1	4	2	3	3	2	3	

Table 4.6: Number of individuals of carabid and cicindelid species as code numbers (see Table 4.1 for actual names) and cumulative number of species (Cum. No.), recorded for each monthly replicate over the first sampling season (June 1994 - May 1995), arranged for each of the four point habitats (17 18 19 20) at site 5. Blank cells indicate no species were recorded in the four point habitats. Total abundance (Tot. Abu.); Total number of species (Tot. No. Sp.).

	June	July	August	Sept	Oct	Nov	Dec	Jan	Feb	March	April	May	Total
Species	21 22 23 24	21 22 23 24	21 22 23 24	21 22 23 24	21 22 23 24	21 22 23 24	21 22 23 24	21 22 23 24	21 22 23 24	21 22 23 24	21 22 23 24	21 22 23 24	
250a						2 2 0 0	0 0 2 0	0 0 2	0 0 2		0 0 0 2		12
35a					0 0 0 2				2 2 0 2	8 0 0 2	2 0 0 2		22
115b	0 2 0 0										26 10 0 0	8 10 0 0	56
178					2 0 0 0								2
243						0 0 4 0	0 0 0 2	0 0 6 2	0 0 2 0	0 0 14 2			32
126											0 0 2 0		2
Tot. Abu.	2	0	0	0	4	8	4	10	10	26	44	18	126
Cu No.	1	1	1	1	3	5	5	5	5	5	6	6	6
Tot. No. Sp.	1	0	0	0	2	2	2	2	3	2	4	1	

Table 4.7: Number of individuals of carabid and cicindelid species as code numbers (see Table 4.1 for actual names) and cumulative number of species (Cum. No.), recorded for each monthly replicate over the first sampling season (June 1994 - May 1995), arranged for each of the four point habitats (21 22 23 24) at site 6. Blank cells indicate no species were recorded in the four point habitats. Total abundance (Tot. Abu.); Total number of species (Tot. No. Sp.).

	June	July	August	Sept	Oct	Nov	Dec	Jan	Feb	March	April	May	Total
Species	25 26 27 28	25 26 27 28	25 26 27 28	25 26 27 28	25 26 27 28	25 26 27 28	25 26 27 28	25 26 27 28	25 26 27 28	25 26 27 28	25 26 27 28	25 26 27 28	
40a							2 0 0 0						2
115a	24 3 0 3	0 0 0 3		0 0 0 3	3 0 0 0	12 6 0 3	0 0 0 3						63
126	6 30 12 0	0 21 0 0	0 39 12 0	3 42 87 0	0 57 93 0	27 177 63	21 51 6 12			0 12 3 0			774
130b	3 0 0 0					3 0 0 3							9
133	6 0 0 0							0 0 0 3		0 0 3 0			12
154		3 0 0 0				0 3 0 0							6
115b		0 3 0 0	6 0 3 0	6 3 6 3	3 0 0 0	48 15 0 15	39 0 0 6	6 6 0 3	0 3 3 0 0	3 30 54 0	3 9 9 0	0 3 3 0	318
178					3 0 0 0	3 0 0 0							6
257						6 0 0 0							6
160		0 6 3 0	0 12 0 0	0 9 3 0	0 60 12 0	6 15 3 0	0 3 0 3		0 0 6 0				141
147											0 3 0 0		3
256						0 0 3 0							3
Tot. Abu.	87	39	72	165	231	411	146	18	39	105	24	6	1343
Cu No.	4	7	7	7	8	10	11	11	11	11	12	12	
Tot. Sp. No.	4	5	3	4	5	9	5	2	2	3	2	1	

Table 4.8: Number of individuals of carabid and cicindelid species as code numbers (see Table 4.1 for actual names) and cumulative number of species (Cum. No.), recorded for each monthly replicate over the first sampling season (June 1994 - May 1995), arranged for each of the four point habitats (25 26 27 28) at site 7. Blank cells indicate no species were recorded in the four point habitats. Total abundance (Tot. Abu.); Total number of species (Tot. No. Sp.).

	June	July	August	Sept	Oct	Nov	Dec	Jan	Feb	March	April	May	Total
Species	29 30 31 32	29 30 31 32	29 30 31 32	29 30 31 32	29 30 31 32	29 30 31 32	29 30 31 32	29 30 31 32	29 30 31 32	29 30 31 32	29 30 31 32	29 30 31 32	
243					0 0 3 0		3 0 0 0			3 0 0 0			9
115b			3 0 0 0			3 0 0 0	3 0 0 0		6 0 0 0	18 3 9 15	45 0 6 15	33 9 0 15	183
126							0 0 0 3		0 3 0 3	3 0 3 0	6 0 0 12		33
133									0 3 0 0				3
Tot. Abu.	0	0	3	0	3	3	9	0	15	54	84	57	228
Cu. No.	0	0	1	1	2	2	3	3	4	4	4	4	
Tot. No. Sp.	0	0	1	0	1	1	3	0	3	3	2	1	

Table 4.9: Number of individuals of carabid and cicindelid species as code numbers (see Table 4.1 for actual names) and cumulative number of species (Cum. No.), recorded for each monthly replicate over the first sampling season (June 1994 - May 1995), arranged for each of the four point habitats (29 30 31 32) at site 8. Blank cells indicate no species were recorded in the four point habitats. Total abundance (Tot. Abu.); Total number of species (Tot. No. Sp.).

Species	June	July	August	Sept	Oct	Nov	Dec	Jan	Feb	March	April	May	Total
115a	33	3	2	3	17	47	11	2	10	18	2	2	150
32	6	4	4	12	26	10	0	10	4	2	0	2	80
252	0	0	0	0	2	2	0	2	2	0	0	0	8
254	0	0	0	0	2	2	4	0	0	0	0	0	8
38	0	0	0	0	0	6	6	10	18	6	10	4	60
213	0	0	4	0	0	28	8	14	26	4	2	0	86
147	0	0	0	0	0	0	0	0	0	4	3	2	9
115b	0	3	12	18	7	81	48	15	41	134	123	81	563
35a	2	0	0	0	0	0	0	0	6	28	10	8	54
45a	0	0	0	0	0	2	0	0	2	0	0	0	4
140	0	0	0	0	0	0	0	0	0	2	0	0	2
178	0	2	0	0	5	3	0	0	0	0	0	0	10
181	0	2	0	0	0	0	0	0	0	0	0	0	2
240a	0	0	4	0	0	0	0	0	0	0	0	2	6
250a	0	0	0	0	14	6	4	2	2	0	2	0	30
250a	0	0	0	0	0	2	0	0	0	0	0	0	2
126	48	21	51	132	152	267	93	0	6	21	20	0	811

Table 4.10: Number of individuals of carabid and cicindelid species as code numbers, (see Table 4.1 for actual names) and cumulative number of species (Cu. No.), recorded over the first sampling season (June 1994 - May 1995), for the whole sampling area, and arranged for each of the 12 monthly replicates. Total abundance (Tot. Abu.); Total number of species (Tot. No. Sp.).

Species	June	July	August	Sept	Oct	Nov	Dec	Jan	Feb	March	April	May	Total
14	0	0	0	0	0	18	2	0	0	0	0	0	20
7	0	0	0	0	0	16	2	0	0	0	0	0	18
150	0	9	12	12	72	28	6	0	6	0	0	0	145
40a	0	0	0	0	0	0	2	0	0	0	0	0	2
40b	0	0	0	0	0	0	2	0	0	0	0	0	2
243	0	0	0	0	39	20	75	14	4	23	0	0	175
105	0	0	0	0	0	0	2	0	6	10	6	2	26
130b	3	0	0	0	0	6	0	0	0	0	0	0	9
133	6	0	0	0	0	0	0	3	3	3	0	0	15
154	0	3	0	0	0	3	0	0	0	0	0	0	6
257	0	0	0	0	0	6	0	0	0	0	0	0	6
256	0	0	0	0	0	3	0	0	0	0	0	0	3
Tot. Abu	98	47	89	177	336	556	265	72	136	255	178	103	2312
Cu. No.	6	11	13	13	17	24	27	27	27	29	29	29	29
Tot. No. Sp.	6	8	7	5	10	20	14	9	14	12	9	8	

Table 4.10: Continued

	June	July	August	Sept	Oct	Nov	Dec	Jan	Feb	March	April	May	Total
Species	1 2 3 4	1 2 3 4	1 2 3 4	1 2 3 4	1 2 3 4	1 2 3 4	1 2 3 4	1 2 3 4	1 2 3 4	1 2 3 4	1 2 3 4	1 2 3 4	
140	2 0 0 0				0 0 0 2								4
147	2 0 0 0			0 0 0 2									4
32			0 0 1 0 0	2 0 0 0	0 2 0 0		0 0 2 0	2 0 2 0					20
115b				2 0 0 0									2
115a					0 0 6 2		0 0 2 0						10
38					0 0 2 0	2 0 2 0	0 2 2 0	0 0 2 0					12
254						2 0 0 0							2
130a											0 0 2 0		2
Tot. Abu.	4	0	10	5	14	6	8	6	0	0	2	0	56
Cum No.	2	2	3	4	6	7	7	7	7	7	8	8	8
Tot. No. Sp.	2	0	1	3	4	2	3	2	0	0	1	0	

Table 4.11: Number of individuals of carabid and cicindelid species as code numbers (see Table 4.1 for actual names) and cumulative number of species (Cum. No.), recorded for each monthly replicate over the second sampling season (June 1995 - May 1996), arranged for each of the four point habitats (1 2 3 4) at site 1. Blank cells indicate no species were recorded in the four point habitats. Total abundance (Tot. Abu.); Total number of species (Tot. No. Sp.).

	June	July	August	Sept	Oct	Nov	Dec	Jan	Feb	March	April	May	Total
Species	5 6 7 8	5 6 7 8	5 6 7 8	5 6 7 8	5 6 7 8	5 6 7 8	5 6 7 8	5 6 7 8	5 6 7 8	5 6 7 8	5 6 7 8	5 6 7 8	
35a			2 0 0 2						0 0 2 0	4 4 2 4	0 2 0 2	0 0 0 2	26
38				0 0 0 4	0 2 2 0	0 4 0 8	0 0 0 4	2 2 8 10	0 0 8 6	0 0 2 4	0 2 0 0		68
213					2 4 2 0	8 4 8 0	2 2 2 0	2 2 4 0	0 0 0 2				44
140						0 0 2 0							2
32						0 0 4 0							4
115a								0 0 0 2					2
115b											0 0 0 2	0 0 0 2	4
Tot. Abu.	0	0	4	4	12	38	10	32	18	20	8	4	150
Cu. No.	0	0	1	2	3	5	5	6	6	6	7	7	7
Tot. No. Sp.	0	0	1	1	2	4	2	3	3	2	3	2	

Table 4.12: Number of individuals of carabid and cicindelid species as code numbers (see Table 4.1 for actual names) and cumulative number of species (Cum. No.), recorded for each monthly replicate over the second sampling season (June 1995 - May 1996), arranged for each of the four point habitats (5 6 7 8) at site 2. Blank cells indicate no species were recorded in the four point habitats. Total abundance (Tot. Abu.); Total number of species (Tot. No. Sp.).

	June	July	August	Sept	Oct	Nov	Dec	Jan	Feb	March	April	May	Total
Species	9 10 11 12	9 10 11 12	9 10 11 12	9 10 11 12	9 10 11 12	9 10 11 12	9 10 11 12	9 10 11 12	9 10 11 12	9 10 11 12	9 10 11 12	9 10 11 12	
140	2 0 0 0												2
155	0 0 2 0												2
115a								0 0 18 0	2 2 0 0	0 0 2 0			24
150										0 2 0 0			2
115b											0 0 2 0		2
35a											0 0 2 4		6
147											0 0 0 4		4
Tot. Abu.	4	0	0	0	0	0	0	18	4	4	12	0	42
Cu. No.	2	2	2	2	2	2	2	3	3	4	7	7	7
Tot. No. Sp.	2	0	0	0	0	0	0	1	1	2	3	0	

Table 4.13: Number of individuals of carabid and cicindelid species as code numbers (see Table 4.1 for actual names) and cumulative number of species (Cum. No.), recorded for each monthly replicate over the second sampling season (June 1995 - May 1996), arranged for each of the four point habitats (9 10 11 12) at site 3. Blank cells indicate no species were recorded in the four point habitats. Total abundance (Tot. Abu.); Total number of species (Tot. No. Sp.).

	June	July	August	Sept	Oct	Nov	Dec	Jan	Feb	March	April	May	Total
Species	13 14 15 16	13 14 15 16	13 14 15 16	13 14 15 16	13 14 15 16	13 14 15 16	13 14 15 16	13 14 15 16	13 14 15 16	13 14 15 16	13 14 15 16	13 14 15 16	
240a		0 2 0 0	0 6 0 0		38 0 0 0	2 0 0 0							48
7					23 0 0 0	8 0 0 0							31
35a					0 0 12 0						0 0 0 2		14
250a						8 0 0 0							8
115a						0 2 0 6			0 0 0 18				26
115a-w							0 0 0 4	4 4 6 10	34 34 12 28	12 6 4 6	0 0 0 4		168
115b									2 2 4 2		0 0 2 2		2
250b						2 0 0 0							2
Tot. Abu.	0	2	6	0	73	28	4	24	126	28	12	0	313
Cu. No.	0	1	1	1	3	6	7	7	8	8	9	9	9
Tot. No. Sp.	0	1	1	0	3	5	1	1	3	1	4	0	

Table 4.14: Number of individuals of carabid and cicindelid species as code numbers, (see Table 4.1 for actual names) and cumulative number of species (Cum. No.), recorded for each monthly replicate over the second sampling season (June 1995 - May 1996), arranged for each of the four point habitats (13 14 15 16) at site 4. Blank cells indicate no species were recorded in the four point habitats. Total abundance (Tot. Abu.); Total number of species (Tot. No. Sp.).

	June	July	August	Sept	Oct	Nov	Dec	Jan	Feb	March	April	May	Total
Species	17 18 19 20	17 18 19 20	17 18 19 20	17 18 19 20	17 18 19 20	17 18 19 20	17 18 19 20	17 18 19 20	17 18 19 20	17 18 19 20	17 18 19 20	17 18 19 20	
243				0 4 0 2	4 44 6 26	4 22 0 32	0 18 0 4						166
130a					0 0 2 0								2
256					0 0 0 4								4
115a						2 0 0 0	2 0 0 0		4 0 0 0				8
105						0 4 0 0	2 0 0 4	2 0 0 0	4 0 0 2				18
115b							2 0 0 0		0 0 0 2				4
240b	0 2 0 0						0 0 2 0						4
35b									2 0 0 0	0 2 0 0			4
Tot. Abu.	2	0	0	6	86	64	34	2	14	2	0	0	210
Cu. No.	1	1	1	2	4	6	7	7	8	8	8	8	8
Tot. No. Sp.	1	0	0	1	3	3	5	1	4	1	0	0	

Table 4.15: Number of individuals of carabid and cicindelid species as code numbers (see Table 4.1 for actual names) and cumulative number of species (Cum. No.), recorded for each monthly replicate over the second sampling season (June 1995 - May 1996), arranged for each of the four point habitats (17 18 19 20) at site 5. Blank cells indicate no species were recorded in the four point habitats. Total abundance (Tot. Abu.); Total number of species (Tot. No. Sp.).

	June	July	August	Sept	Oct	Nov	Dec	Jan	Feb	March	April	May	Total
Species	21 22 23 24	21 22 23 24	21 22 23 24	21 22 23 24	21 22 23 24	21 22 23 24	21 22 23 24	21 22 23 24	21 22 23 24	21 22 23 24	21 22 23 24	21 22 23 24	
115b	8 4 0 0	0 0 0 4							4 4 0 0	0 2 0 0		0 4 0 0	30
243				0 4 12 30	0 8 44 58	4 4 36 28	0 0 4 6						238
35a									0 0 2 0		8 0 0 0		10
Tot. Abu.	12	4	0	46	110	72	10	0	10	2	8	4	278
Cu. No.	1	1	1	2	2	2	2	2	3	3	3	3	3
Tot. No. Sp.	1	1	0	1	1	1	1	0	2	1	0	1	

Table 4.16: Number of individuals of carabid and cicindelid species as code numbers (see Table 4.1 for actual names) and cumulative number of species (Cum. No.), recorded for each monthly replicate over the second sampling season (June 1995 - May 1996), arranged for each of the four point habitats (21 22 23 24) at site 6. Blank cells indicate no species were recorded in the four point habitats. Total abundance (Tot. Abu.); Total number of species (Tot. No. Sp.).

	June	July	August	Sept	Oct	Nov	Dec	Jan	Feb	March	April	May	Total
Species	25 26 27 28	25 26 27 28	25 26 27 28	25 26 27 28	25 26 27 28	25 26 27 18	25 26 27 28	25 25 26 27	24 25 26 27	24 25 26 27	24 25 26 27	24 25 26 27	
115b		0 3 0 0		0 0 6 0	18 0 138 39	21 0 0 6		0 0 3 18	0 0 90 0	0 6 18 0	0 0 9 0		375
126				0 6 12 0	0 18 90 0	3 0 0 0		0 0 6 0	0 0 6 0		0 0 9 0	0 3 0 0	153
150					24 157 87 0	0 0 12 0				0 0 3 0			183
115a									3 0 0 0		0 0 9 0		12
133											0 0 3 3		6
276											0 0 3 0		3
Tot. Abu.	0	3	0	24	471	42	0	27	99	27	36	3	732
Cu. No.	0	1	1	2	3	3	3	3	4	4	6	6	6
Tot. No. Sp.	0	1	0	2	3	3	0	2	3	2	5	1	

Table 4.17: Number of individuals of carabid and cicindelid species as code numbers (see Table 4.1 for actual names) and cumulative number of species (Cum. No.), recorded for each monthly replicate over the second sampling season (June 1995 - May 1996), arranged for each of the four point habitats (25 26 27 28) at site 7. Blank cells indicate no species were recorded in the four point habitats. Total abundance (Tot. Abu.); Total number of species (Tot. No. Sp.).

	June	July	August	Sept	Oct	Nov	Dec	Jan	Feb	March	April	May	Total
Species	29 30 31 32	29 30 31 32	29 30 31 32	29 30 31 32	29 30 31 32	29 30 31 32	29 30 31 32	29 30 31 32	29 30 31 32	29 30 31 32	29 30 31 32	29 30 31 32	
115b			8 0 0 2	14 0 2 0		6 0 2 0	2 0 2 0	2 0 4 0	0 0 2 0	2 0 8 0			56
126				2 0 0 0	0 0 0 2				0 0 2 0	0 0 6 0			12
35a	8 2 0 0	2 0 2 0							14 0 4 0	4 0 0 0			36
Tot. Abu.	10	4	10	18	2	8	4	6	22	20	0	0	104
Cu. No.	1	1	2	3	3	3	3	3	3	3	3	3	3
Tot. No. Sp.	1	1	1	2	1	1	1	1	3	3	0	0	

Table 4.18: Number of individuals of carabid and cicindelid species as code numbers (see Table 4.1 for actual names) and cumulative number of species (Cum. No.), recorded for each monthly replicate over the second sampling season (June 1995 - May 1996), arranged for each of the four point habitats (29 30 31 32) at site 8. Blank cells indicate no species were recorded in the four point habitats. Total abundance (Tot. Abu.); Total number of species (Tot. No. Sp.).

Species	June	July	August	Sept	Oct	Nov	Dec	Jan	Feb	March	April	May	Total
115a	0	0	0	0	8	10	4	20	29	2	9	0	82
32	0	0	10	2	2	4	2	4	0	0	0	0	24
252	0	0	0	0	0	0	0	0	0	0	0	0	0
254	0	0	0	0	0	2	0	0	0	0	0	0	2
38	0	0	0	4	6	16	8	24	14	6	2	0	80
213	0	0	0	0	8	20	6	8	2	0	0	0	44
147	2	0	0	2	0	0	0	0	0	0	4	0	8
115b	12	7	10	24	195	35	6	27	112	36	17	6	487
35a	10	4	4	0	12	0	0	0	22	18	20	2	92
45a	0	0	0	0	0	0	0	0	0	0	0	0	0
140	4	0	0	0	2	2	0	0	0	0	0	0	8
178	0	0	0	0	0	0	0	0	0	0	0	0	0
181	0	0	0	0	0	0	0	0	0	0	2	0	2
240a	0	2	6	0	38	2	0	0	0	0	0	0	48
250a	0	0	0	0	0	8	0	0	0	0	0	0	8
250b	0	0	0	0	0	2	0	0	0	0	0	0	2
126	0	0	0	20	110	3	0	6	8	6	9	3	165
14	0	0	0	0	0	0	0	0	0	0	0	0	0
7	0	0	0	0	23	8	0	0	0	0	0	0	31
150	0	0	0	0	168	12	0	0	0	5	0	0	185
40a	0	0	0	0	0	0	0	0	0	0	0	0	0
40b	0	0	0	0	0	0	0	0	0	0	0	0	0
243	0	0	0	52	190	130	32	0	0	0	0	0	404
105	0	0	0	0	0	4	6	2	6	0	0	0	18
130b	0	0	0	0	0	0	0	0	0	0	0	0	0
133	0	0	0	0	0	0	0	0	0	0	6	0	6
154	0	0	0	0	0	0	0	0	0	0	0	0	0
257	0	0	0	0	0	0	0	0	0	0	0	0	0
256	0	0	0	0	4	0	0	0	0	0	0	0	4
35b	0	0	0	0	0	0	0	0	2	2	0	0	4
130a	0	0	0	0	2	0	0	0	0	0	2	0	4
155	2	0	0	0	0	0	0	0	0	0	0	0	2
115a-w	0	0	0	0	0	0	4	24	108	28	4	0	168
240b	2	0	0	0	0	0	2	0	0	0	0	0	4
276	0	0	0	0	0	0	0	0	0	0	3	0	3
Tot. Abu.	32	13	30	104	768	258	70	115	303	103	78	11	1885
Cu.No.	6	7	8	9	17	21	22	22	23	23	26	26	26
Tot. No. Sp.	6	3	4	6	14	15	9	8	9	8	11	3	

Table 4.19: Number of individuals of carabid and cicindelid species as code numbers (see Table 4.1 for actual names) and cumulative number of species (Cu. No.), recorded over the second sampling season (June 1995 - May 1996), for the whole sampling area, and arranged for each of the 12 monthly replicates. Total abundance (Tot. Abu.); Total number of species (Tot. No. Sp.).

Species	June	July	August	Sept	Oct	Nov	Dec	Jan	Feb	March	April	May	Total
115a	33	3	2	3	25	57	15	22	39	20	11	2	232
32	6	4	14	14	28	14	2	14	4	2	0	2	104
252	0	0	0	0	2	2	0	2	2	0	0	0	8
254	0	0	0	0	2	4	4	0	0	0	0	0	10
38	0	0	0	4	6	22	14	34	32	12	12	4	140
213	0	0	4	0	8	48	14	22	28	4	2	0	130
147	2	0	0	2	0	0	0	0	0	4	7	2	17
115b	12	10	22	42	202	116	54	42	153	170	140	87	1050
35a	12	4	4	0	12	0	0	0	28	46	30	10	146
45a	0	0	0	0	0	2	0	0	2	0	0	0	4
140	4	0	0	0	2	2	0	0	0	2	0	0	10
178	0	2	0	0	5	3	0	0	0	0	0	0	10
181	0	2	0	0	0	0	0	0	0	0	2	0	4
240a	0	2	10	0	38	2	0	0	0	0	0	2	54
250a	0	0	0	0	14	14	4	2	2	0	2	0	38
250b	0	0	0	0	0	4	0	0	0	0	0	0	4
126	48	21	51	152	262	270	93	6	14	27	29	3	976
14	0	0	0	0	0	18	2	0	0	0	0	0	20
7	0	0	0	0	23	24	2	0	0	0	0	0	49
150	0	9	12	12	240	40	6	0	6	5	0	0	330
40a	0	0	0	0	0	0	2	0	0	0	0	0	2
40b	0	0	0	0	0	0	2	0	0	0	0	0	2
243	0	0	0	52	229	150	107	14	4	23	0	0	579
105	0	0	0	0	0	4	8	2	12	10	6	2	44
130b	3	0	0	0	0	6	0	0	0	0	0	0	9
133	6	0	0	0	0	0	0	3	3	3	6	0	21
154	0	3	0	0	0	3	0	0	0	0	0	0	6
257	0	0	0	0	0	6	0	0	0	0	0	0	6
256	0	0	0	0	4	3	0	0	0	0	0	0	7
35b	0	0	0	0	0	0	0	0	2	2	0	0	4
130a	0	0	0	0	2	0	0	0	0	0	2	0	4
155	2	0	0	0	0	0	0	0	0	0	0	0	2
115a-w	0	0	0	0	0	0	4	24	108	28	4	0	168
240b	2	0	0	0	0	0	2	0	0	0	0	0	4
276	0	0	0	0	0	0	0	0	0	0	3	0	3
Tot. Abu.	130	60	119	281	1104	814	335	187	439	358	256	114	4197
Cu. No.	11	16	17	19	25	30	33	33	34	34	35	35	35
Tot. No. Sp.	11	10	8	8	18	23	17	12	16	15	14	9	

Table 4.20: Sum of the number of individuals of carabid and cicindelid species as code numbers (see Table 4.1 for actual names) and cumulative number of species (Cu. No.), recorded over the two sampling seasons (June 1994 - May 1996), for the whole sampling area, and arranged for each of the 12 monthly replicates. Total abundance (Tot. Abu.); Total number of species (Tot. No. Sp.).

No.	Species	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8	Totals
1	115a	39	6	2	30	10	0	63	0	150
2	32	14	56	10	0	0	0	0	0	80
3	252	2	6	0	0	0	0	0	0	8
4	254	6	0	2	0	0	0	0	0	8
5	38	2	58	0	0	0	0	0	0	60
6	213	6	80	0	0	0	0	0	0	86
7	147	4	0	0	0	2	0	3	0	9
8	115b	0	4	0	2	0	56	318	183	563
9	35a	0	30	0	0	2	22	0	0	54
10	45a	0	0	4	0	0	0	0	0	4
11	140	0	0	2	0	0	0	0	0	2
12	178	0	0	0	2	0	2	6	0	10
13	181	0	0	0	2	0	0	0	0	2
14	240a	0	0	0	6	0	0	0	0	6
15	250a	0	0	0	16	2	12	0	0	30
16	250b	0	0	0	2	0	0	0	0	2
17	126	0	0	0	2	0	2	774	33	811
18	14	0	0	0	20	0	0	0	0	20
19	7	0	0	0	18	0	0	0	0	18
20	150	0	0	0	4	0	0	141	0	145
21	40a	0	0	0	0	0	0	2	0	2
22	40b	0	0	0	2	0	0	0	0	2
23	243	0	0	0	0	134	32	0	9	175
24	105	0	0	0	0	26	0	0	0	26
25	130b	0	0	0	0	0	0	9	0	9
26	133	0	0	0	0	0	0	12	3	15
27	154	0	0	0	0	0	0	6	0	6
28	257	0	0	0	0	0	0	6	0	6
29	256	0	0	0	0	0	0	3	0	3
TOTAL NO. OF SPECIES		7	7	5	12	6	6	12	4	
TOTAL ABUNDANCE		73	240	20	106	176	126	1343	228	2312

Table 4.21. Number of individuals of carabid and cicindelid species as code numbers (see Table 4.1 for actual names) recorded over the first sampling season (June 1994 - May 1995), for the whole sampling area, arranged for each of the eight sites (1-8).

No.	Species	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8	Total
1	115a	10	2	24	26	8	0	12	0	82
2	32	20	4	0	0	0	0	0	0	24
3	252	0	0	0	0	0	0	0	0	0
4	254	2	0	0	0	0	0	0	0	2
5	38	12	68	0	0	0	0	0	0	80
6	213	0	44	0	0	0	0	0	0	44
7	147	4	0	4	0	0	0	0	0	8
8	115b	2	4	2	14	4	30	375	56	487
9	35a	0	26	6	14	0	10	0	36	92
10	45a	0	0	0	0	0	0	0	0	0
11	140	4	2	2	0	0	0	0	0	8
12	178	0	0	0	0	0	0	0	0	0
13	181	0	0	0	2	0	0	0	0	2
14	240a	0	0	0	48	0	0	0	0	48
15	250a	0	0	0	8	0	0	0	0	8
16	250b	0	0	0	2	0	0	0	0	2
17	126	0	0	0	0	0	0	153	12	165
18	14	0	0	0	0	0	0	0	0	0
19	7	0	0	0	31	0	0	0	0	31
20	150	0	0	2	0	0	0	183	0	185
21	40a	0	0	0	0	0	0	0	0	0
22	40b	0	0	0	0	0	0	0	0	0
23	243	0	0	0	0	166	238	0	0	404
24	105	0	0	0	0	18	0	0	0	18
25	130b	0	0	0	0	0	0	0	0	0
26	133	0	0	0	0	0	0	6	0	6
27	154	0	0	0	0	0	0	0	0	0
28	257	0	0	0	0	0	0	0	0	0
29	256	0	0	0	0	4	0	0	0	4
30	35b	0	0	0	0	4	0	0	0	4
31	130a	2	0	0	0	2	0	0	0	4
32	155	0	0	2	0	0	0	0	0	2
33	115a-w	0	0	0	168	0	0	0	0	168
34	240b	0	0	0	0	4	0	0	0	4
35	276	0	0	0	0	0	0	3	0	3
Total No. of Species		8	7	7	9	8	3	6	3	
Total Abundance		56	150	42	313	210	278	732	104	1885

Table 4.22. Number of individuals of carabid and cicindelid species as code numbers (see Table 4.1 for actual names) recorded over the second sampling season (June 1995 - May 1996), for the whole sampling area, arranged for each of the eight sites (1-8).

No.	Species	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8	Total
1	115a	49	8	26	56	18	0	75	0	232
2	32	34	60	10	0	0	0	0	0	104
3	252	2	6	0	0	0	0	0	0	8
4	254	8	0	2	0	0	0	0	0	10
5	38	14	126	0	0	0	0	0	0	140
6	213	6	124	0	0	0	0	0	0	130
7	147	8	0	4	0	2	0	3	0	17
8	115b	2	8	2	16	4	86	693	239	1050
9	35a	0	56	6	14	2	32	0	36	146
10	45a	0	0	4	0	0	0	0	0	4
11	140	4	2	4	0	0	0	0	0	10
12	178	0	0	0	2	0	2	6	0	10
13	181	0	0	0	4	0	0	0	0	4
14	240a	0	0	0	54	0	0	0	0	54
15	250a	0	0	0	24	2	12	0	0	38
16	250b	0	0	0	4	0	0	0	0	4
17	126	0	0	0	2	0	2	927	45	976
18	14	0	0	0	20	0	0	0	0	20
19	7	0	0	0	49	0	0	0	0	49
20	150	0	0	2	4	0	0	324	0	330
21	40a	0	0	0	0	0	0	2	0	2
22	40b	0	0	0	2	0	0	0	0	2
23	243	0	0	0	0	300	270	0	9	579
24	105	0	0	0	0	44	0	0	0	44
25	130b	0	0	0	0	0	0	9	0	9
26	133	0	0	0	0	0	0	18	3	21
27	154	0	0	0	0	0	0	6	0	6
28	257	0	0	0	0	0	0	6	0	6
29	256	0	0	0	0	4	0	3	0	7
30	35b	0	0	0	0	4	0	0	0	4
31	130a	2	0	0	0	2	0	0	0	4
32	155	0	0	2	0	0	0	0	0	2
33	115a-w	0	0	0	168	0	0	0	0	168
34	240b	0	0	0	0	4	0	0	0	4
35	276	0	0	0	0	0	0	3	0	3
Total No. of Species		10	8	10	14	11	6	13	5	
Total Abundance		129	390	62	419	386	404	2075	332	4197

Table 4.23: Sum of the number of individuals of carabid and cicindelid species as code numbers (see Table 4.1 for actual names) recorded for the two sampling seasons (June 1994 -May 1996), arranged for each of the eight sites (1-8).

Sp.	S1				S2				S3				S4				S5				S6				S7				S8				Tot.	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32		
115a	4	0	33	2	6	0	0	0	0	0	0	2	2	14	6	8	8	2	0	0	0	0	0	0	0	39	9	0	15	0	0	0	0	150
32	2	2	2	8	18	19	3	16	0	8	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	80
252	0	0	0	2	2	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	
254	2	0	4	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	
38	0	0	2	0	2	24	0	32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	60	
213	4	2	0	0	40	30	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	86	
147	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	3	0	0	0	0	0	0	9	
115b	0	0	0	0	2	2	0	0	0	0	0	0	0	0	0	2	0	0	0	0	4	22	0	0	114	72	105	27	111	12	15	45	563	
35a	0	0	0	0	0	2	0	28	0	0	0	0	0	0	0	0	0	2	0	0	12	2	0	8	0	0	0	0	0	0	0	0	54	
45a	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	
140	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	
178	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	2	0	0	0	6	0	0	0	0	0	0	0	10	
181	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	
240a	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	
250a	0	0	0	0	0	0	0	0	0	0	0	0	2	6	2	6	0	2	0	0	2	2	6	2	0	0	0	0	0	0	0	0	30	
250b	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	
126	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	2	0	57	429	276	12	9	3	3	18	811	

Table 4.24: Number of individuals of carabid and cicindelid species (sp.) as code numbers, (see Table 4.1 for actual names) recorded over the first sampling season (June 1994 - May 1995), for the whole sampling area, arranged for each of the 32 point habitats, for the eight sites (S1-S8). Total abundance (Tot. Abu.); Total number of species (Tot. No. Sp.).

Sp.	S1				S2				S3				S4				S5				S6				S7				S8				Tot
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	
1150	0	0	8	2	0	0	0	2	2	2	20	0	0	2	0	24	8	0	0	0	0	0	0	0	3	0	9	0	0	0	0	0	82
32	4	2	14	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	24
252	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
254	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
38	2	2	8	0	2	10	20	36	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	80
213	0	0	0	0	14	12	16	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	44
147	2	0	0	2	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8
115b	2	0	0	0	0	0	0	4	0	0	2	0	2	2	6	4	2	0	0	2	12	14	0	4	39	9	264	63	34	0	20	2	487
35a	0	0	0	0	6	6	4	10	0	0	2	4	0	0	12	2	0	0	0	0	8	0	2	0	0	0	0	0	28	2	6	0	92
45a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
140	2	0	0	2	0	0	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8
178	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
181	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
240a	0	0	0	0	0	0	0	0	0	0	0	0	40	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	48
250a	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8
250b	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
126	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	27	123	0	2	0	8	2	153	
14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 4.25: Number of individuals of carabid and cicindelid species (sp.) as code numbers, (see Table 4.1 for actual names) recorded over the second sampling season (June 1995 - May 1996), for the whole sampling area, arranged for each of the 32 point habitats, for the eight sites (S1-S8). Total abundance (Tot. Abu.); Total number of species (Tot. No. Sp.).

Sp.	S1				S2				S3				S4				5				S6				S7				Tot.				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28		29	30	31	32
115a	4	0	41	4	6	0	0	2	2	2	20	2	2	16	6	32	16	2	0	0	0	0	0	0	42	9	9	15	0	0	0	0	232
32	6	4	16	8	18	19	3	20	0	8	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	104	
252	0	0	0	2	2	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	
254	4	0	4	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	
38	2	2	10	0	4	34	20	68	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	140	
213	4	2	0	0	54	42	16	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	130	
147	2	4	0	2	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	2	0	0	0	0	0	3	0	0	0	0	0	17	
115b	2	0	0	0	2	2	0	4	0	0	2	0	2	2	6	6	2	0	0	2	46	36	0	4	153	81	369	90	145	12	35	47	1050
35a	0	0	0	0	6	8	4	38	0	0	2	4	0	0	12	2	0	2	0	0	20	2	2	8	0	0	0	0	28	2	6	0	146
45a	0	0	0	0	0	4	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	
140	2	0	0	2	0	0	2	0	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	
178	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	2	0	0	0	6	0	0	0	0	0	0	10	
181	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	
240a	0	0	0	0	0	0	0	0	0	0	0	0	44	8	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	54	
250a	0	0	0	0	0	0	0	0	0	0	0	0	10	6	2	6	0	2	0	0	2	2	6	2	0	0	0	0	0	0	0	38	
250b	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	
126	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	2	0	60	456	399	12	11	3	11	20	976
14	0	0	0	0	0	0	0	0	0	0	0	0	10	0	2	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	
7	0	0	0	0	0	0	0	0	0	0	0	0	35	4	2	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	49	

Table 4.26: Sum of the number of individuals of carabid and cicindelid species (sp.) as code numbers, (see Table 4.1 for actual names) recorded over the two sampling seasons (June 1994 - May 1996), for the whole sampling area, arranged for each of the 32 point habitats, for the eight landscape elements (S1-S8). Total abundance (Tot. Abn.); Total number of species (Tot. No. Sp.).

Sp.	S1			S2			S3			S4			S5			S6			S7			Tot.										
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21		22	23	24	25	26	27	28	29	30	31
150	0	0	0	0	0	0	0	0	0	0	2	0	0	0	2	2	0	0	0	0	0	0	0	0	30	162	129	3	0	0	0	330
40a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	2
40b	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
243	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	24	114	42	120	4	16	122	128	0	0	0	0	6	0	579	
105	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	24	6	0	14	0	0	0	0	0	0	0	0	0	0	44	
130b	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	9	
133	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	6	6	0	3	0	21	
154	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	3	0	0	0	0	0	6	
257	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	6	
256	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	3	0	0	0	0	7	
35b	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	4	
130a	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	4	
155	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	
115a-w	0	0	0	0	0	0	0	0	0	0	0	0	50	44	22	52	0	0	0	0	0	0	0	0	0	0	0	0	0	0	168	
240b	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	0	0	0	0	0	0	0	0	0	0	0	4	
276	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	
Tot. Abu.	26	12	71	20	92	109	45	144	4	16	28	14	157	80	56	126	70	128	46	142	74	56	132	142	314	714	918	129	190	20	55	67
No. Sp.	8	4	4	6	7	6	5	6	2	4	5	5	8	6	9	12	5	6	3	5	5	4	4	4	10	6	7	6	4	4	4	2

Table 4.26: Continued

**APPENDIX 3: PHOTOGRAPHS OF SOME OF THE
LARGER CARABIDS AND
CICINDELIDS COLLECTED**



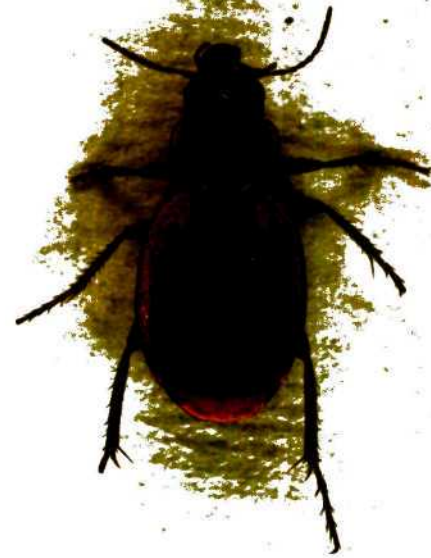
Cicindela marginella Dej.
(spp.) *inanis* (Wallengr.)



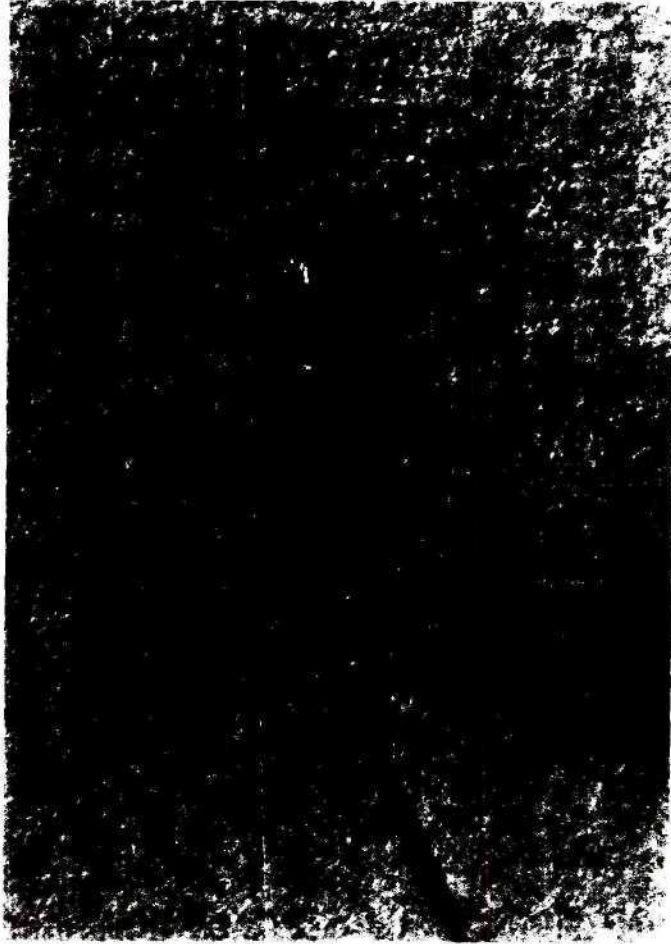
Dromica gilvipes Boh.



Dromica tuberculata Dej.
(spp.) *carinulata* (Chaud.)



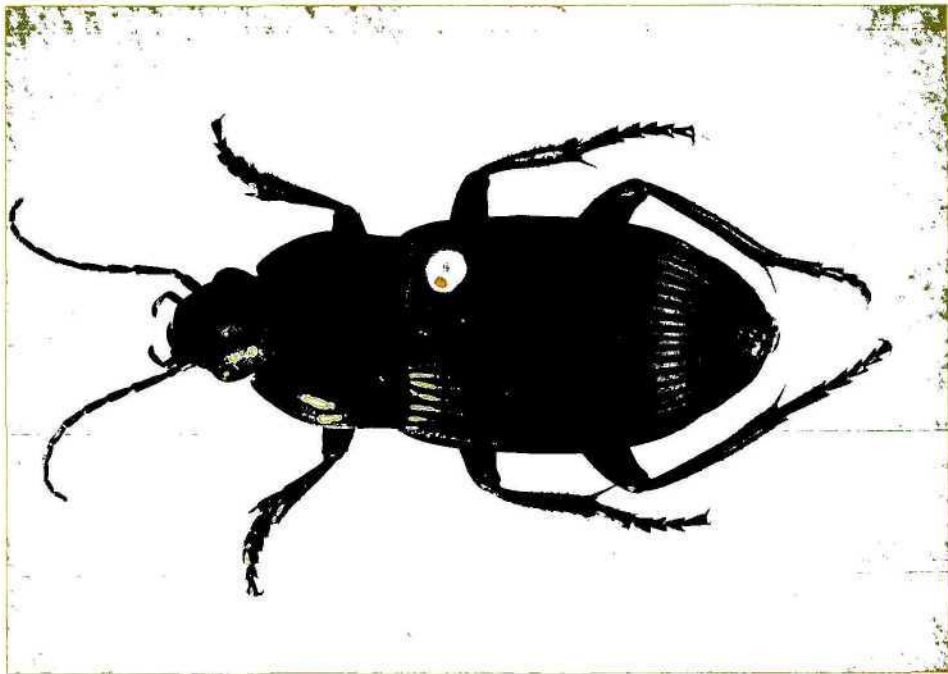
Graphipterus cordiger Dej.
(spp.) *subhamatus* (Basil.)



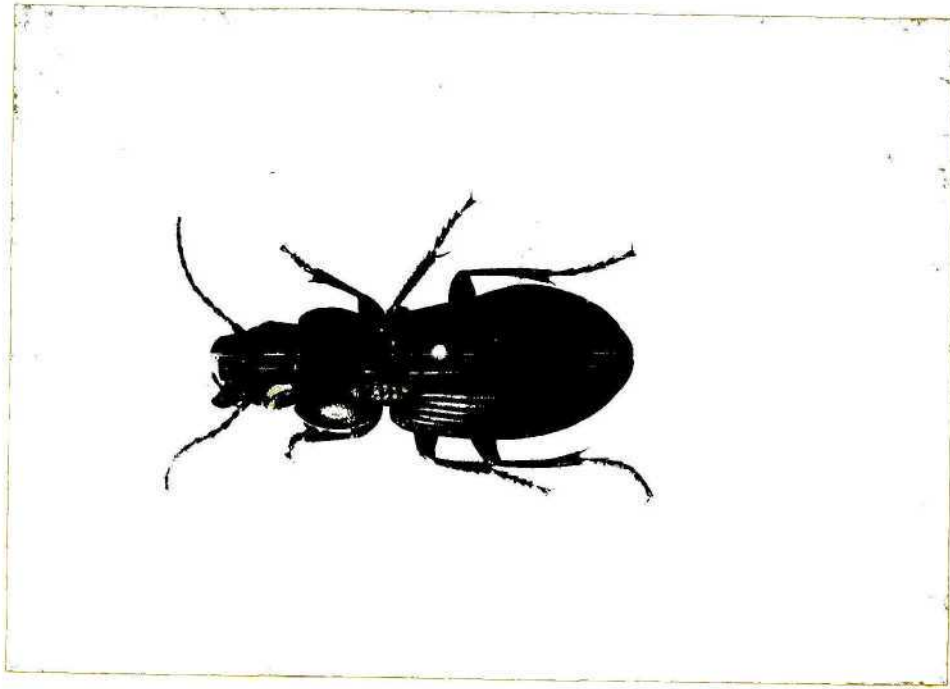
Euleptus caffer Boh.



Metagonum gilvipes Boh.



Carabidae species (243)



Cychrus species (244)



Craspidophorus bonvouloiri Chaud.



Pachydinodes bipustulatus Boh.



Harpaliini species (115b)



Chlaeniostenus cylindricus Dej.



Craspidophorus impictus Boh.



Hystrichopus atratus Chaud.