Factors affecting millipede, centipede and scorpion diversity in a savanna environment

by

David James Druce

Submitted in fulfilment of the academic requirements for the degree of
Master of Science in the
School of Life and Environmental Sciences
University of Natal
Durban

December 2000

Abstract

Millipedes, centipedes and scorpions are an important component of the ground-dwelling invertebrate fauna, and may have value as bioindicators of ground-dwelling invertebrate diversity. However, some level of understanding of which factors influence patterns of their distribution and diversity is necessary prior to any investigation of their use in conservation planning and as bioindicators. This project was undertaken in the Greater Makalali Conservancy in the Northern Province. Many methods have been used to sample millipedes, centipedes and scorpions but the efficiency of these in savanna has not been investigated. One aim was to determine a method for quantitatively sampling these invertebrates in this environment. Six sampling methods were tested during the study. Millipedes were found to be efficiently sampled by active searching $9m^2$ quadrats and drive transects, centipedes by actively searching $25m^2$ plots and scorpions by pitfall traps. The other methods tested were wet cloths and cryptozoan traps. Another aim was to determine spatial and temporal variation in millipede, centipede and scorpion diversity in the range of habitat types present in the Conservancy. 45 sites within five habitat types were sampled during three different sampling periods. The highest diversity for each study group was recorded in the most heterogeneous habitat, with the lowest being recorded in more homogeneous habitat types. Millipede and centipede diversity was significantly influenced by habitat type, while sampling period had a significant effect on millipede and scorpion diversity. Quantifying the effect of various environmental factors on the diversity of these invertebrates was a further aim. Maps of various Conservancy wide variables as well as micro-habitat variables were created, including an accurate vegetation map, maps of soil characteristics, rainfall and temperature. Micro-habitat characteristics were also recorded within each of the sample sites. Diversity of the three study groups was related to specific micro-habitat variables. A Geographic Information Systems (GIS) model was created, predicting millipede, centipede and scorpion diversity in areas of the Conservancy not sampled. Three undescribed millipede and one centipede species were found and a new distribution record for a scorpion species was documented. These results emphasise the importance of invertebrate biodiversity studies in the savanna environment.

Preface

The work described in this dissertation was carried out in the School of Life and Environmental Sciences, University of Natal, Durban, from January 1999 to December 2000, under the supervision of Dr. M.L. Hamer and Dr. R.H. Slotow.

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

D.J. Druce December 2000

CONTENTS

List of tables

List of Figures

Acknowledgements

I would like to express my sincere thanks to all that were involved in this project and who made it possible and as enjoyable as it was.

Firstly to my supervisors Dr. Michelle Hamer (UNP) and Dr. Rob Slotow (UND), I would like to thank you both for making this project possible and sparking an interest in invertebrate research. Thank you also for all the help, ideas and guidance that you provided throughout the project.

To all those in the Greater Makalali Conservancy, Northern Province, South Africa.
Thanks to Charles Smith, Bernie Smith and Ross Kettles for allowing me to work in the Conservancy and for showing an interest in the project and savanna research in general.
Also to those who, during the last two years, have been involved in Makalali Research; Jonathan Braak, Sophie Greatwood and Audrey Delsink. It has been excellent working with you all and you have all taught me a great deal about the bush amongst other things. Jon, you'll need to come to Makalali some time, there's still plenty of piscatorial research that needs to be done. Soph, thanks for the friendship, all the hard work and for keeping us going on all the elephant and vegetation transects. Without your help, determination and encouragement, it would have been a lot more difficult to complete. Auds, thanks for your friendship, for all the work that you've put into the project and for giving assistance beyond that which was needed.
Thanks also to Guy and Donnie from Garonga for helping at various stages, for your input and for your great hospitality.

To everyone who has worked in the Conservancy over the past two years, I thank you all for making my trips so enjoyable. It has been great getting to know such awesome people and spending time with you all. Thanks for the great friendships that have been forged over these past few years. It's often the people at a reserve that make that reserve what it is and you all have made it a second home for me. Thanks a million! I look forward to working with you all in the coming years.

Thanks very much to Bruce Page for all his help with the vegetation data analysis, the construction of the vegetation map and helpful comments on various parts of the project.
Thanks also to Frank Sokolic for his patience and all his hours of assistance with different GIS problems.

Thanks also to Michelle Hamer (millipedes), Marzio Zapparoli (centipedes) and Lorenzo Prendini (scorpions) for all the invertebrate identifications.

To Cheryl Whitmore, who spent so much time in Makalali with me. Thanks for all the hard work that you put in whilst up in Makalali and for all the organising and cooking. Thanks also for always patiently giving of your time to help with statistics and other difficulties I had in my project! All the best for the future, I know you will do well in everything that you do.

To Markus Clarke and Peter Williams. Thank you both for all the help that you gave in the weeks you were in Makalali. It was great having others to help and the work could not have been done without your assistance. Markus, thanks for adding a bit of muscle on all those occasions we had to push start 'Bam-bam'.

To those who came up to Makalali from UND and UNP (Chantal, Tarryne, Guy, Wayne, Navashni, Claire, Yvonne, Carol, Sean and Kavish) during the time that I spent there. Thanks very much for helping out and for making each trip interesting and enjoyable. I've enjoyed spending time with you all in the bush and I hope that some of you will decide to work in savanna research.

Thanks also to those who have been on all the other field trips that I've been involved in over the period of my MSc. I hope you've all enjoyed them and had as great a time as I have. You've all helped make the last two years as great and enjoyable as they have been. I hope to see many of you working in savanna research in the coming years.

A very special thanks to Debbie Donkin, with whom an office was shared for so many long hours during writing up and the final stages of the project. Thanks for providing a great sense of humour and for always being prepared to help, listen and provide comments and discussion about various issues. It would have been a lot more difficult writing up if there had not been someone else around who was going through the same process.

Finally, thanks to my family and friends who have supported and helped me in the last few years and constantly kept me up to date on what was happening back in the bustling metropolis of Durbs! A special thanks to my family for all the support, encouragement and food they provided during the writing up stages of the project and for the time they spent error checking

parts of the project. Everything was greatly appreciated! Thanks also to all those others who showed an interest in my work and provided encouragement during the last few months of the project.

Thanks to Martiens Pelser and Colleen du Plessis of the Computer Foundation, Pretoria for providing the digital elevation data.

The vegetation sampling was funded by Distillers Corporation as part of the Amarula Elephant Research Programme.
This project was supported by a National Research Foundation (NRF) grant to Dr. M. Hamer (GUN number 2034942) and Graduate Assistance bursaries, from the University of Natal, Durban to D. Druce.

CHAPTER 1
GENERAL INTRODUCTION

This chapter aims to introduce the concept of biodiversity, its importance, how it is measured and the relationship between scale and biodiversity. The use of Geographic Information Systems (GIS) as an analytical tool in biodiversity studies will also be introduced. Invertebrate diversity studies in general will be discussed first, followed by a brief discussion on diversity studies in the focal groups of this project, millipedes, centipedes and scorpions. Previous studies dealing with the distribution and diversity of these groups and the influence of various factors on their diversity at different scales will also be discussed. The chapter concludes by discussing the study site and the biome in which it occurs and introducing the aims and objectives of the study.

Biodiversity

What is biodiversity?

Although the terms 'biodiversity' and 'diversity' are widely used, there have not been many clear definitions of what is meant by these terms. They refer to a very complex and all-embracing concept that can be interpreted and analysed at a number of levels and scales (Pearce & Moran, 1994). Biological diversity (biodiversity) refers to the variety of the earth's organisms, including their genetic diversity and the assemblages they form (Reid & Miller, 1989). This implies that there are three levels at which biodiversity is defined; genetic, species and ecosystem levels (Ehrlich & Wilson, 1991; Beck, 1998). Genetic diversity refers to the genetic variation within and between populations of a single species of organisms (Groombridge, 1992), while species diversity refers to the variety of living species (Biodiversity Series 1, 1993). Ecosystem diversity refers to the variety of habitats, biotic communities, and ecological processes as well as the diversity present within ecosystems in terms of habitat differences and the variety of ecological processes (Biodiversity Series 1, 1993).

Species diversity is relatively easier to collect data on than genetic and ecosystem diversity and may also encompass most of the variation observed in biodiversity (Beck, 1998). As a result, this study focuses on determining species level diversity and does not deal with either of the other two levels of diversity. Although it may seem easier to collect data on species diversity as opposed to genetic and ecosystem diversity, there is often little known about the biology of the

species under study. This is especially the case in invertebrate diversity research in southern Africa. Studies, therefore, need to be undertaken to determine how the diversity of various organisms relate to the environment before invertebrate diversity can be used as an indicator of environmental conditions and change.

Importance of biodiversity

The interest in diversity, especially over the past few years, has focused on how diversity influences ecosystems and ecological processes (Tilman, 1999). Ninety five percent of experimental studies support a positive relationship between diversity and ecosystem functioning (Purvis & Hector, 2000) although it has been suggested that diversity is not the driver of this relationship (McCann, 2000). Higher levels of biodiversity have been shown to lead to greater productivity in plant communities, greater nutrition retention in ecosystems and greater ecosystem stability (Naeem, Thompson, Lawler, Lawton & Woodfin, 1994; McCann, 2000; Tilman, 2000). Species diversity also increases the resistance of communities to disease (Purvis & Hector, 2000) and can contribute to climatic stability (van Jaarsveld & Chown, 1996), maintenance of ecosystems (van Jaarsveld & Chown, 1996) and recovery from unpredictable events (Biodiversity Series 1, 1993) through the life forms that are supported.

Various hypotheses have been suggested for the observation that more diverse communities are more stable. One of these hypotheses states that because there are more species in a more diverse ecosystem, the odds are greater that at least some species will respond preferentially to particular conditions and perturbations (averaging effect) (McCann, 2000). The negative covariance model, however, states that a more diverse ecosystem will have greater odds of containing some species that are capable of replacing functionally important species (McCann, 2000). Communities may also be more stable when there are more species, as this results in a greater number of weak interactions between species thus dampening the potentially destabilising strong interactions that would exist between species if there were only a few species present (Ives, Gross & Klug, 1999; McCann, 2000). As a result, the world's biota are vitally important in forming the life-support system for the earth (Brussard *et al.*, 1997).

Ehrlich and Wilson (1991) suggest two other reasons for the conservation of biodiversity: (1) its conservation is ethical and aesthetic and (2) there are huge direct economic benefits that can be derived from biological resources. Biological resources are elements of biodiversity that can be directly used from the environment. They include all the food that humans eat, as well as many

medicines and industrial products such as wood (Ehrlich & Wilson, 1991; Biodiversity Series 1, 1993). As there are still many areas in the world where not enough research has been done, there is still potential for the discovery of biological resources that can be of benefit to humans. In South Africa, a large proportion of the population is directly dependent on biological resources for subsistence. These resources include the gathering, harvesting or hunting of animals and plants for food, medicine, shelter, fuel, building materials and trade (White Paper on Biodiversity, 1997). By conserving biodiversity within the country, these resources and their uses can be retained.

Social benefits include recreation and tourism (Biodiversity Series 1, 1993). Many conserved areas are used extensively for recreation, and this activity can also be used as a way in which funds can be generated for the further protection and maintenance of the protected areas. It is in this way that ecotourism in South Africa is dependent on biodiversity. Areas in the country that contain a high biodiversity are likely to be visited by more tourists as they can see a large variety of species in one area and in the shortest possible time.

Need to manage biodiversity

Management is required to conserve biodiversity. In order to do this effectively, the greatest number of species need to be supported at the least cost (Myers, Miltermeier, Miltermeier, da Fonseca & Kent, 2000). This involves selecting areas of high biodiversity and conserving them. The only way that society and governments can make informed decisions about the importance of preserving specific areas is by having scientifically accurate information about the diversity and ecological relationships of the fauna (Goodman & Lanyon, 1994). High quality biodiversity surveys should be carried out in order to assist in selecting areas to protect (Balmford & Gaston, 1999) and then within these protected areas, to determine areas that can be used for various activities and areas that should be left untouched because of their importance in biodiversity conservation. This ensures that reserve systems are not bigger than is necessary, available resources are not spread too thinly and that conservation objectives are more likely to be met (Balmford & Gaston, 1999).

Many countries, including South Africa, are signatories to the Convention on Biological Diversity. This means that South Africa has committed itself to *inter alia* (1) conserving the existing biodiversity for future generations, (2) using biological resources in a sustainable manner and (3) ensuring a fair and equitable sharing of benefits derived from the use of genetic

resources (van Jaarsveld & Chown, 1996). In order to accomplish these aims, present biodiversity needs to be determined and biodiversity monitoring needs to proceed. This is not an easy task, as South Africa is one of the most biologically diverse countries in the world (Pienaar, 1991; White Paper on Biodiversity, 1997). The country also supports a large variety of endemic species (e.g. Hamer, 1997). As a result, methods that enable the rapid assessment of biodiversity need to be determined, especially for the 'hyperdiverse' terrestrial groups such as some of the invertebrate groups (Colwell & Coddington, 1994). These sampling methods also need to be standardised for particular groups of organisms in order to allow the comparison of diversity between different areas. I will test the effectiveness and efficiency of sampling methods that have been used to sample millipedes, centipedes and scorpions in order to determine which methods can be used in the rapid biodiversity assessment of these invertebrate groups.

Measuring diversity

Although different levels of biodiversity organisation exist, most analyses of spatial variation in biodiversity have been undertaken at the species level (Groombridge, 1992; Trueman & Cranston, 1997; Gaston, 2000). However, as species diversity consists of both the number of individuals in a species (richness) and how these species abundances are distributed among the various species (evenness) (Ludwig & Reynolds, 1988), both richness and evenness need to be considered. Both these indices can be incorporated into a single index referred to as a diversity index.

Although there are a number of diversity indices that have been used in ecology, Shannon's index has been the most widely used (Ludwig & Reynolds, 1988; Krebs, 1989). This index 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 (Ludwig & Reynolds, 1988). This average 'uncertainty' increases as the number of species increases and as the distribution of individuals among the species becomes even (Ludwig & Reynolds, 1988).

Shannon's Index is given by the equation,

$$H' = - \sum_{i=1}^{s^*} (p_i \ln p_i)$$

where H' is the average 'uncertainty' per species in an infinite community made up of S^*

species with known proportional abundances $p_1, p_2, p_3, ..., p_s$. (Ludwig & Reynolds, 1988).

As a result, the units of measurement for Shannon's diversity index are not species. However, a set of diversity numbers, Hill's diversity numbers, measure the effective number of species in a sample and are, therefore, probably easier to interpret ecologically (Ludwig & Reynolds, 1988). Hill's number N1, is given by the following equation,

$$N1 = e^{H'}$$

where H' is Shannon's Index.

This number determines the effective number of species as a measure of the number of species in the sample where each species is weighted by its abundance (Ludwig & Reynolds, 1988). In the case of N1, the number is weighted by the number of abundant species (Ludwig & Reynolds, 1988).

There are also a number of different evenness indices. Some of these indices are dependent on sample size (Ludwig & Reynolds, 1988) and are therefore not the best indices to use. Ludwig and Reynolds (1988) suggest that the modified Hill's ratio (referred to as E5) is the best index as it is independent of the sample size. This equation is given by:

$$E5 = \frac{(1/\lambda)-1}{e^{H'}} = \frac{N2}{N1}$$

where N1 and N2 are Hill's diversity indices and λ is Simpson's index (Ludwig & Reynolds, 1988).

N2 is defined by the following equation:

$$N2 = 1/\lambda$$

And λ by the following equation:

$$\lambda = \sum_{i=1}^{s} p_i^2$$

where p_i is the proportional abundance of the ith species, given by:

$$p_i = \frac{n_i}{N} \quad , \qquad i = 1,2,3,\ldots, S$$

where n_i is the number of individuals of the ith species and N is the known number of individuals for the S species in the population (Ludwig & Reynolds, 1988).

In this study I measure richness, evenness and diversity indices at the species level for millipedes, centipedes and scorpions.

Biodiversity indicators

In order to provide an indication of the potential diversity of certain areas and to compare them with others, indicator groups may be used. McGeoch (1998) describes three types of indicators; environmental, ecological and biodiversity indicators. In this study the type of indicator which is relevant is a biodiversity indicator. A biodiversity indicator is a group of taxa (e.g. genus, tribe, family or order, or a selected group of species from a range of higher taxa), or functional group, the diversity of which reflects some measure of the diversity of other higher taxa in a habitat or set of habitats (McGeoch, 1998). Biodiversity indicators will be species-rich in areas that are species-rich in general (Faith & Walker, 1996) and will, therefore, save the time and expense that would be necessary for comprehensive biodiversity surveys (McGeoch, 1998). Invertebrates are particularly suited for use as indicators because of their high species diversity, their occurrence and their importance in the functioning of natural ecosystems (Rosenberg, Danks & Lehmkuhl, 1986). They have not been extensively used in biodiversity studies in the past due to the general lack of suitable taxonomic keys, the small size and cryptic colouration of most invertebrates as well as the perception that they are not economically viable to study and sample (Rosenberg *et al.*, 1986). Invertebrates as well as any other group should only be used as biodiversity indicators in cases when they are readily identifiable and where there is relatively good taxonomic knowledge of the group (Samways, 1994). As there is a lack of covariance in the species richness of higher taxa, care also has to be taken in trying to extrapolate from one group to another (Gaston, 2000). Some insect groups that have been used as indicators in the past include butterflies (Beccaloni & Gaston, 1995) and tiger beetles (Rodriguez, Pearson & Barrera, 1998).

I will test whether either millipede, centipede or scorpion diversity can be used as a diversity indicator for any of the other two groups of invertebrates.

Scale & diversity

Insight into distribution patterns of species is fundamental to an understanding of the biogeography and ecology of that species (Judas & Hauser, 1998). However, the distribution and diversity of species often differs between scales as their distribution is controlled by abiotic and biotic components in the environment, and the relative importance of these factors in regulating community patterns varies with spatial scale (Menge & Olson, 1990; Gaston, 2000). Biotic factors are those environmental influences which are related to living organisms, while abiotic factors are environmental influences produced other than by living organisms (Bush, 1997). Many studies that deal with biodiversity are concerned with local scale and the processes that drive biodiversity within those scales. However, processes at some scales, such as the regional scale, may influence the patterns observed at other scales, such as the local scale (Gaston, 2000). As a result, species distribution patterns are dependent on a complex interplay between both large- and local-scale processes (Menge & Olson, 1990) and need to be analysed at different spatial scales, from the home range of a single individual to the global range of the species (Judas & Hauser, 1998).

Diversity often varies within a site (local scale), among sites in a region (mesoscale) and among regions (global or geographic scale) (Menge & Olson, 1990). In the case of global biodiversity, Gaston (2000) states that a large proportion of regional variation can be explained in terms of a few environmental (i.e. abiotic) variables. These variables include latitudinal gradients, environmental energy and in the case of aquatic environments, depth gradients (Gaston, 2000). These variables do not, however, fully explain all the patterns as they do not include biotic influences and there is no pattern that is without variation and exception (Gaston, 2000).

Although local scale patterns and biodiversity may be generally governed by regional scale processes, there are other variables that influence biodiversity on a smaller scale. One would expect the diversity of organisms that burrow to be influenced by the spatial distribution of suitable soil types. Dangerfield and Telford (1992) have, for example, shown that small scale variation in certain abiotic components in an area may produce significant heterogeneity in the composition and abundance of soil fauna. In their natural miombo woodland study site in Marondera, they found that change in the vegetation structure, litter fall and soil properties

resulted in a significant heterogeneity in the composition and abundance of all soil fauna (Dangerfield & Telford, 1992). As a result, one needs to determine whether large-scale processes can be used as an instrument for studying the underlying processes which may operate at smaller scales (Purvis & Hector, 2000) and how patterns observed at one scale may relate to those observed at other scales (Gaston, 2000).

Due to these different scales and the variation in patterns between them, the development of any predictive model will need to begin with simple local-scale models moving up to more complex larger-scale models (Menge & Olson, 1990). Biodiversity studies will, therefore, need to attempt to determine if the relationships observed at a small scale can be extrapolated to a larger scale. This is especially important for groups that have limited dispersal ability or movement ranges such as soil invertebrates. However, most studies on diversity and scale effects have focused on larger species, such as vertebrates (e.g. herbivores, Beardall, Joubert & Retief, 1984; Melton, 1987) or invertebrate species that disperse well (e.g. butterflies, DeVries, Walla & Greeney, 1999). In this study I will determine the effects of scale on diversity and processes affecting diversity at both the local scale (i.e. between habitats) and the habitat scale (i.e. within habitats).

GIS as an analytical tool

The process of determining and documenting the variation in patterns between scales has been facilitated by the development of Geographic Information Systems (GIS). GIS are computer hardware and software packages designed to store, analyse or manipulate and display spatially referenced data (Haslett, 1990; Fabricius & Coetzee, 1992; Michelmore, 1994; Barr & Carter, 1995). Multiple data layers can be analysed and displayed (Yonzon, Jones & Fox, 1991). GIS uses two types of systems, the raster and vector-based systems. Raster-based systems record spatial information as points in a regular network of grid cells, while vector-based systems use patterns of points, lines and areas to represent the data (Haslett, 1990).

As GIS has the ability to integrate a variety of information about an area in question, it has a wide variety of applications in research and management. It is a highly adaptable mapping and analysis system, which can easily cope with a wide range of geographical, ecological and biological data sets (Haslett, 1990). The advent of GIS has allowed scientists to obtain correlations between the range limits of plants and animals and extremes of temperature, precipitation, wind and other factors (Barr & Carter, 1995). GIS can therefore be used to relate

the biodiversity of an area to the biotic and abiotic factors of that area. Once the biodiversity of an area has been sampled, it can be mapped and analysed through the use of GIS. It also provides a powerful tool for wildlife managers facing issues of increasing complexity (Michelmore, 1994).

GIS has been used to model the habitats of a wide variety of organisms. Different factors important in habitat selection have been used to model habitat selection of organisms or the potential impact of different land uses on the habitat distribution of organisms. Yonzon *et al.* (1991) used GIS to assess the habitat and estimate the population of Red Pandas in Langtang National Park in Nepal. Three factors were used to determine the core areas for Panda habitation in the park. These were land use, land cover and elevation and direction of the slope (Yonzon *et al.*, 1991). From these results the population of Pandas in the Park and the risk of local extinction based on the present land use in the Park was estimated. Kadmon & Heller (1998) used GIS and multivariate analysis to determine to what climatological factors, land snail fauna were correlated. They determined that the patterns in faunal variation were significantly correlated to underlying variation in rainfall (Kadmon & Heller, 1998). I will use GIS to determine the relationship between millipede, centipede and scorpion diversity at the local level (between habitats) and as a tool for modelling diversity in areas at the local scale where diversity has not been measured.

Invertebrates

Current knowledge - invertebrates versus vertebrates

The Insecta have always been regarded as the most speciose class in the Animal Kingdom (Ehrlich & Wilson, 1991; Samways, 1993; Myers *et al.*, 2000). This class also constitutes a substantial proportion of terrestrial species' richness and biomass, and plays a significant role in ecosystem functioning (McGeoch, 1998). Even so, known species diversity is only a small fraction of the total species diversity (Ehrlich & Wilson, 1991; Myers *et al.*, 2000). The southern African sub-region is no different to the global situation; invertebrates have been neglected relative to the vertebrates and in many cases the taxonomic and biogeographic databases for invertebrates are scattered, outdated, incomplete or simply non-existent (Pienaar, 1991; Hamer, 1997). As a result, these data are useless to conservationists and planners (Hamer, 1997).

Samways (1993) has suggested two reasons for this discrepancy in research between vertebrates and invertebrates. The first impediment to insect conservation is taxonomic, in that probably only about 7-10% of insects are known to science (Samways, 1993). As a result of this poor knowledge of the taxonomy and distribution of invertebrates, scientists are unable to identify them to species level and thereby access information on their biology and distribution. The other is the strongly warped perception of the value of insects, in that they are generally viewed as being a nuisance and are preferred dead (Samways, 1993). However, all of this is beginning to change as conservation agencies, especially in South Africa, are changing their mission statements to include an aim of determining and conserving the biodiversity of areas under their control. This has all come about through the need to conserve all biodiversity (as set out in the Convention of Biological Diversity) and the realisation of the importance of invertebrates within ecosystems.

As the invertebrates are such a diverse and speciose group of organisms, studies on their diversity and factors affecting it need to be focused on specific groups. In this study, millipedes, centipedes and scorpions were chosen as the three focal groups because (1) their taxonomy is fairly well known and experts are available for species level identification, (2) they represent different functional groups (detritivores and predators) and may, therefore, be influenced by different environmental variables and (3) they have a limited dispersal ability, with the result that scale effects can be determined.

Millipede biology and sampling

The southern African sub-region contains a high number of millipede species. The Diplopoda (millipedes) comprises one of the largest classes in the Animal Kingdom and is the third largest in the terrestrial arthropods, following the Insecta and Arachnida (Kime & Golovatch, 2000). A total of 552 millipede species, distributed between 71 genera, 15 families and 7 orders have been recorded in Africa south of the Zambezi and Kunene Rivers (Hamer, 1998). Although millipede biodiversity is relatively well documented in South and Southern Africa (Hamer, 1997), there are many areas in this region which have not been sampled. There is also collecting bias throughout the sub-region, with Kwa-Zulu Natal having received greater attention due to the work of R.F. Lawrence (Hamer, 1997). As millipedes have limited powers of dispersal and a high degree of speciation, the evolution of a large number of endemics with restricted ranges has occurred (Hopkin & Read, 1992). As a result of this, as well as previous collecting bias, there is potential for the existence of undiscovered species.

In the southern African region, the millipede knowledge base is relatively large in comparison to that of many of the other soil invertebrates. This, combined with the fact that when millipedes are limited by a single edaphic factor (e.g. soil texture, litter thickness), they will generally fail to overcome it, even though other ecological factors may be favourable (Kime & Golovatch, 2000), resulting in them having the potential to act as important umbrella species or biological indicators in the protection of more obscure elements of the soil fauna (Hamer, 1997). Each species of millipede also has an ecological preference which limits it to a particular habitat (Kime, 1992). In Australia, however, they cannot be recommended as environmental indicators, because although they are common, conspicuous, diverse, easily collected and are sensitive to environmental perturbations, there is not enough information about their general biology (Black, 1997). This is also the case in southern Africa, where most of the work on millipedes has focused on ascertaining the distribution of species rather than determining how they are distributed through the environment (local scale) or how different environmental factors may limit their distribution. Some authors have, however, undertaken studies on the ecology of certain millipede species. This includes work on their importance in soil fertility (Dangerfield & Telford, 1989), the seasonal activity patterns of Julid millipedes (Dangerfield & Telford, 1991) and millipede behaviour in a savanna habitat (Dangerfield & Kaunda, 1994).

Millipedes play an important role in the soil formation process (Bano, 1992). Dangerfield (1990) states that detritis feeders (of which millipedes form a part) may process up to 30% of the annual dead organic matter input to most soils and affect the decomposition of this material through fragmentation, inoculation with microbial spores and physical disturbance. Millipedes have been shown in other experiments to play an important role in the formation of humus, as they feed on and break down woody debris as well as decaying leaves (Lawrence, 1984; Shear, 1999).

A number of different methods have been used to sample millipedes, with most sampling having been carried out in closed canopy environments as opposed to the more open savanna environment. Sampling methods that have been used include pitfall trapping (Dangerfield & Telford, 1991; Kime, 1992; Klinger, 1992; Tarasevich, 1992; Mesibov, Taylor & Brereton, 1995; Trueman & Cranston, 1997), cryptozoan traps (Madari, Kiss & Korsos, 1996), sorting of litter (Tarasevich, 1992) or soil samples (Klinger, 1992) and active or hand searching (Klinger, 1992; Tarasevich, 1992; Mesibov *et al.*, 1995).

Centipede Biology and Sampling

There are about 150 species of centipede in South Africa, while there are about 2000 species in the world (Lawrence, 1984). They fall into four orders, all of which are represented in South Africa (Lawrence, 1984). These are Geophilomorpha (earth centipedes), Lithobiomorpha (stone centipedes), Scolopendromorpha (large centipedes) and Scutigeromorpha (house centipedes) (Lawrence, 1984). Because of the different habitats these different types of centipedes live in, each is limited by slightly different environmental factors.

Centipedes are a potentially important group of organisms for ecological studies in that their diversity seems to show a good correlation with habitat characteristics of certain vegetation types (Zapparoli, 1992a). They are also sensitive to changes in the environment and because of their long life cycles and predatory nature, they could serve as indicators of change in the environment (Kos, 1992). Zapparoli (1992a) states that more knowledge on the centipede general ecology is required before they can be used in studies of environmental quality definition in Central Italy. This is, however, not just the case for the centipedes of that area, but also for centipedes throughout the world.

Sampling for centipedes seems to have focused on the use of two main methods. These are the use of pitfall traps, (Klinger, 1992; Trueman &Cranston, 1997; Wytwer, 1992; Zapparoli, 1992a) and active searching under surface debris (Klinger, 1992; Wytwer, 1992; Zapparoli, 1992b). Other searching methods such as the searching of soil samples for centipedes (Klinger, 1992; Wytwer, 1992) and the sieving of leaf litter (Wytwer, 1992) have also been used in the past.

Scorpion Biology and Sampling

Not much work has been done on the biology and distribution of scorpions in South Africa. Most of the early studies conducted in South Africa were carried out by two scientists; G. Newlands and R.F. Lawrence. There are 2 scorpion families in South Africa, the Buthidae and Scorpionidae (Newlands, 1978). One of the more detailed studies on scorpion distribution was undertaken by Lawrence in the Kruger National Park, South Africa. He recorded 20 scorpion species in the Park (Lawrence, 1964). Not many of the species were found to be widespread in the Park, although there were four robust species which were suggested to be distributed throughout the Park (Lawrence, 1964).

Although there is a dearth of knowledge about scorpion ecology and behaviour (Polis, 1990b), scorpions may be important species in biodiversity studies for a number of reasons. In some habitats they appear to be one of the most successful predators in terms of density, diversity, standing biomass and their role in community energetics and structure (Polis, 1990a). Their spatial distribution and range are also governed by a number of factors. Polis (1990b) suggests that some of the physical factors that limit their distribution include temperature, precipitation, soil or rock characteristics, stone or litter cover and environmental physiognomy. Some of these factors may be brought about as a result of the different sheltering methods employed by scorpions.

Scorpions have two main methods of sheltering. These are burrowing or hiding under rocks, stones or bark. Within the *Parabuthus* genus (one of the largest genera of Buthids in South Africa) some species are burrowers and dig burrows in sandy or sandy loam soils, while others find shelter beneath stones, logs or other debris (Newlands, 1978). These *Parabuthus* species are also not found in areas where the average annual rainfall exceeds 600mm (Newlands, 1978). Other genera, such as *Opisthophthalmus* which burrows, are limited by soil hardness (Lamoral, 1979). Their distribution, range and habitat selection is directly correlated with soil hardness and to a much lesser and variable extent, soil texture, but not specific geological composition of the soil (Lamoral, 1979). The *Uroplectes* species have the widest distribution of all the Buthid scorpions and shelter under stones, beneath the bark of trees and in the cracks and crevices of old tree stumps (Newlands, 1978). It would be expected that those species that live under surface debris or rocks would be limited by the availability of potential shelters.

Different methods have been used to sample scorpions. One of those that have been used fairly extensively is that of active searching. During the day, active searching involves turning over surface objects (rocks, logs and other debris) and looking under the loose bark of trees or other ground cover (Eastwood, 1978; Sissom, Polis & Watt, 1990; Warburg, 1997). Active searching at night, however, involves the use of ultra-violet lights (Sissom *et al.*, 1990; Warburg, 1997). Scorpions fluoresce under ultra-violet light and are therefore relatively easy to detect at night (Polis, 1990b). Pitfall traps have also been used to sample scorpions (Sissom *et al.*, 1990; Margules, Milkovits & Smith, 1994).

Savanna

The savanna biome covers over half the land surface in Africa and one fifth of the land surface of the world (Scholes & Walker, 1993). In southern Africa it occupies 46% of the area, whilst in South Africa it covers over one-third of the country (Low & Rebelo, 1996; Stuart-Hill & Tainton, 1999). It has developed in the arid to semi-arid (350mm to 900mm summer rainfall) northern and eastern parts of the country where there are high temperatures and a pronounced dry winter period (Stuart-Hill & Tainton, 1999).

Savannas are characterised by a grassy ground layer and a distinct upper layer of woody plants (Low & Rebelo, 1996; Tainton, 1999). The tree layer usually consists of a discontinuous crown cover of 2 to 10 metres, which overlies a grassy layer 0.5 to 2 metres tall (Scholes, 1997). There may be an intermediate layer of small trees or shrubs present, and the grass layer may be temporarily absent or replaced by dicotyledonous herbs during drought or other disturbance (Scholes, 1997). Tree density varies greatly from conditions approaching forest through to almost open grassland (Tainton, 1999). In South Africa there are two basic categories of savanna. These are the broad- and fine-leafed savannas (Scholes, 1997). The broad-leafed savannas predominate where there are nutrient-poor and moist areas, while the fine-leafed savannas are usually found on nutrient-rich, drier areas (Scholes, 1997).

The savanna biome is important for grazing, fuelwood, timber and other resources (Scholes, 1997). It forms the main location of the livestock and ecotourism industries and contain a high faunal diversity. This is due to the high plant diversity within this biome (Scholes & Walker, 1993).

Although they constitute the most extensive African biome and are so important, savannas are the least studied terrestrial system (Scholes & Walker, 1993).

The Greater Makalali Conservancy as a study site

The Greater Makalali Conservancy is situated in the foothills of the Drakensberg Mountains in the Northern Province of South Africa. It was formed in 1993 by the initial purchase of 7 500ha of cattle ranchland. Over the years the Conservancy has been extended by the acquisition of adjacent farms and now exceeds 14 500ha. Large mammals have been reintroduced to the Conservancy, including a pride of lion, five white rhino and two herds of elephant translocated

from the Kruger National Park in May 1994. All introduced groups of animals have settled in well and are reproducing successfully.

The Conservancy was previously used for cattle farming and overgrazing has occurred in various parts. This, together with other factors, has resulted in the encroachment of some woody plants in certain areas. This encroachment has caused the development of thickets that would not normally occur in these areas and has resulted in a decrease of available grasses and grasslands. In order to restore the Conservancy to a state similar to what it would have been before the cattle farming, areas are continuously being cleared of the invading woody plants. All the fences have been removed between the previous farms, allowing the animals to move freely throughout the Conservancy. Certain roads that are not needed have also been closed and allowed to re-vegetate. The introduction of some of the large mammals that would have been present in the area before it was converted to ranchland will also assist in restoring the Conservancy to a stage similar to that prior to cattle farming. Large mammals promote patchiness and structural heterogeneity in the reserve because of their variety in size and diet (Cumming, 1982). One of the animals most likely to affect the vegetation is elephant. Elephant have been shown in the past to open up savanna woodlands by pushing over or uprooting trees and shrubs (Cumming, 1982). Management practices also affect the structure and state of the Conservancy. No areas in the Conservancy were burnt prior to October 2000. However, some clearings had been mowed on a yearly basis in an attempt to promote new growth in the grass cover and simulate grazing by large herbivores.

The Greater Makalali Conservancy is situated on the Lowveld plain at an altitude of between 300 and 500m above sea-level. The landscape is a combination of undulating terrain and rocky outcrops. The Conservancy is found within the savanna biome of southern Africa. The main vegetation types are Mixed Lowveld Bushveld (Low & Rebelo, 1996, Type 19) and Mopane Bushveld (Low & Rebelo, 1996, Type 10). The Conservancy contains only one river, the Makhutswi River, a perennial tributary of the Olifants River. Within this riverine belt there is a high diversity of tree species. This river splits the Conservancy and runs from west to east, through the Conservancy. Artificial waterpoints have been created in the Conservancy with some of them being supplied with borehole water, especially during the dry winter months.

Makalali is a relatively dry area with an average annual rainfall of 450mm. Most of the rains fall in the summer months between October and March. Temperatures in the reserve vary between 3°C in winter to above 36°C in summer.

The Conservancy is ecotourism orientated with an emphasis on providing information to the guests about the smaller components of the ecosystem. As a result, this study will serve as a source of information for rangers, who will then be able to inform the tourists about some of the invertebrates of the Conservancy and their importance in the savanna ecosystem.

Aims and objectives of the study

The aims of this project are to determine the most effective methods to efficiently sample millipedes, centipedes and scorpions in the savanna environment and to determine how environmental factors at different scales within the Greater Makalali Conservancy influence their diversity and distribution. The relationship of these environmental factors to the invertebrate diversity will then be used to produce GIS models predicting millipede, centipede and scorpion diversity in areas of the Conservancy that have not been sampled.

In order to determine and describe differences between local scale environmental variables and the distribution of a group of organisms, the accurate measurement and description of local scale variation in factors likely to influence their diversity is required. Ground-dwelling invertebrates, such as millipedes, centipedes and scorpions, are limited in their dispersal ability, with the result that very accurate measurements are required to determine variation between and within habitats. As a result, chapter two deals with the construction of accurate maps of abiotic and biotic components of the Greater Makalali Conservancy. These variables include vegetation, rainfall, temperature and a range of different soil components.

The third chapter assesses six methods that can be used to sample millipedes, centipedes and scorpions and determines which is the most effective and efficient for sampling these organisms in the savanna environment. These include both active and passive sampling methods. Chapter four determines and describes spatial differences in millipede, centipede and scorpion diversity and distribution between five physiognomic habitats in the Conservancy and quantifies temporal variation in millipede, centipede and scorpion diversity. Chapter five is focused at a smaller scale, the micro-habitat scale. The processes determining millipede, centipede and scorpion distribution within a habitat are investigated. This is achieved by determining to what extent specific micro-habitat variables affect their diversity. The relationship between millipede, centipede and scorpion diversity and these micro-habitat variables, will then be used in a Geographic Information System to model diversity of these three groups in parts of the Conservancy where no sampling has taken place. The final chapter is a summarising chapter,

where the implications of this study to further biodiversity studies and the conservation of millipedes, centipedes and scorpions are presented.

CHAPTER 2
VEGETATION, EDAPHIC AND CLIMATIC VARIATION IN THE GREATER MAKALALI CONSERVANCY

Introduction

The distribution and abundance of all organisms is governed by the distribution of environmental conditions and resources on which they are dependent. These resources and environmental conditions are, however, non-uniformally distributed, temporally and spatially. This results in the heterogeneous distribution of the organisms that are influenced by the resources and conditions. These non-uniform, spatial and temporal distribution of resources and abiotic factors influencing the distribution of organisms are referred to as environmental patterns (Addicott, Aho, Antolin, Padilla, Richardson & Soluk, 1987). As these environmental patterns are important in affecting many ecological processes and phenomena (Addicott *et al.*, 1987), a good knowledge of these patterns is vital before the relationships and interactions between organisms and their environment can be accurately determined and described.

One of the most important environmental variables influencing the distribution of many organisms has long been considered to be vegetation. As a result, in many conservation areas one of the most important resources for management is the availability of a good vegetation map. This provides managers with basic information about the ecology of the area and serves as the basis for the compilation of efficient management programs (Whateley & Porter, 1983; Bezuidenhout, 1995). Successful management depends to a large extent on the knowledge of the composition of the vegetation, the extent to which it is being used and the changes that take place in response to differential use by herbivores and fire (Walker, 1976). Vegetation maps provide managers with a good basis with which to identify fairly quickly and accurately areas that need special management, such as burning or clearing and to aid in determining the carrying capacity and potential species composition of the conservation area.

In the past, management strategies, especially in conservation areas, have concentrated on managing large mammal communities and protecting vegetation communities. However, since the Convention of Biological Diversity, the emphasis of conservation agencies has shifted from primarily conserving mammal diversity to determining and conserving the diversity of other groups, such as the invertebrates. However, in order to conserve these groups, the determinants of their diversity and the factors affecting their distribution need to be known. Fine scale

vegetation maps are, therefore, important in these studies as they provide a detailed description of the woody component of the primary producers and are the first step to quantifying structure, diversity and production on a fine scale.

One of the most common methods used to produce vegetation maps has been that of identifying landscape, physiographic or physiognomic units in aerial photographs and then sampling to determine the exact plant species composition within these areas (Walker, 1976; Whateley & Porter, 1983; Goodman, 1990; Brown & Bredenkamp, 1994; Bezuidenhout, 1995; Brown, Bredenkamp & van Rooyen, 1995; Brown, Bredenkamp & van Rooyen, 1996). Fieldwork is required to fix the boundaries of the various plant communities (Whateley & Porter, 1983). However, once the species composition and density is known for a given patch, that area needs to be classified according to a common classification system. Many different types of vegetation classifications based on vegetation structure, physiognomy and broad ecological attributes have been used in the past (Edwards, 1983). These have varied between regions. However, in 1983 Edwards proposed a classification technique for the vegetation of southern Africa. This definition is based on a set of dominant primary growth form types, cover, height and partly on substrata (Edwards, 1983). This technique is in line with similar classifications, but also takes into account local kinds of vegetation by using specialised terms (Edwards, 1983).

Vegetation descriptions exist at different scales. Low and Rebelo (1996) revised descriptions by J.P.H. Acocks in 1953 of the vegetation of South Africa, Lesotho and Swaziland and described vegetation types within the biomes of these areas at a regional scale. Using these descriptions the Greater Makalali Conservancy falls under the two broad vegetation types of Mixed Lowveld Bushveld (Low & Rebelo, 1996, Type 19) and Mopane Bushveld (Low & Rebelo, 1996, Type 10). Mixed Lowveld Bushveld is characterised by a large number of tree species including *Combretum apiculatum* and *C. zeyheri*, *Sclerocarya birrea*, *Acacia nigrescens* and within the shrub layer by species such as *Cissus cornifolia*, *Dichrostachys cinerea*, *Acacia exuvialis* and *Dalbergia melanoxylon* (Low & Rebelo, 1996). The Mopane Bushveld is characterised by a fairly dense growth of *Colophospermum mopane* trees and mixtures of *Colophospermum mopane* and *Combretum apiculatum*. These are associated with a number of other tree species including *Acacia nigrescens*, *Commiphora* spp. and *Terminalia prunioides* (Low & Rebelo, 1996). These two broad vegetation types, however, describe vegetation at a regional scale and as a result do not provide clarification on the actual density and detailed species composition of vegetation at a local scale. Studies at a local scale are therefore required in order to produce this information.

Although vegetation may be one of the most important and most obvious contributors to environmental patterns in the distribution of organisms, there are also other factors that also influence these patterns. These include factors such as water availability (Scholes & Walker, 1993), certain soil characteristics which influence the nutritional status of plants (Bredenkamp, Theron & van Vuuren, 1983; Scholes & Walker, 1993), altitude (Ward, Olsvig-Whittaker & Lawes, 1993) and the underlying geology (Ward *et al.*, 1993). Within the savanna biome, it has been suggested that the maintenance of collective biodiversity is dependent on the temporal and spatial variability of the main savanna determinants (rainfall, soil nutrients, fire and herbivory) and other disturbance (Scholes & Walker, 1993).

At the local scale, factors such as soil characteristics, rainfall, vegetation structure and composition, as well as temperature may affect the distribution and differential use of patches by certain organisms. Because different organisms respond to environmental heterogeneity in different ways and to different degrees, the study of environmental patterns needs to involve the description of the spatial distribution of all resources and abiotic conditions (Addicott *et al.*, 1987) that may affect their distribution.

Prior to the initiation of this project, the Greater Makalali Conservancy did not have a vegetation map or descriptions of any other Conservancy-wide variables that may have aided in determining processes operating within the Conservancy. Some of the Conservancy managers have compiled rough vegetation maps of certain sections of the reserve, based purely on where they observed distinct vegetation boundaries to be. The collection of detailed data on biotic and abiotic factors (vegetation structure and composition, soil characteristics, rainfall and elevation data) within the Conservancy was required in order to assist with effective management and allow for detailed, accurate small scale invertebrate research projects.

The aim of Chapter Two was to quantify the biotic and abiotic factors, present over the Greater Makalali Conservancy, which could influence the diversity of invertebrates. This would need to be accurate at a small scale, to allow one to determine relationships between invertebrate species distribution and diversity at the micro-habitat scale. Objectives were firstly, to produce a detailed fine scale vegetation map for the Greater Makalali Conservancy, which would sub-divide broad vegetation types resulting in smaller vegetation patches of known species composition, density and structure. Secondly, other Conservancy-wide environmental and micro-habitat factors would be mapped accurately at a small scale and quantified and then their relationship to the vegetation and other environmental factors determined. The development of

these data would allow for the quantified analysis of processes and effects on invertebrate diversity as well as enabling those carrying out various other research projects to identify areas that would be important to their research and to accurately compare findings between various vegetation types.

Methods

Construction of the vegetation map

The first step in producing the vegetation map was to produce a physiognomic map of the Conservancy from aerial photographs. 1:60 000 stereo black and white aerial photographs (strip 2, photo 068 & strip 3 photos 113 & 115), taken in September 1997, of the area surrounding and including the Greater Makalali Conservancy were obtained from the Chief Directorate Surveys and Mapping in Mowbray, South Africa. For this study, physiognomic types were defined and separated based on structural differences, as described below. Physiognomic type boundaries were traced onto tracing paper. These resulting traced images were scanned into a computer and saved as a bitmap image. They were imported into Cartalinx GIS programme (Clark Labs), georeferenced (to latitude longitude reference system) and used as a backdrop, from which a digital image of the habitat boundaries could be created on-screen. This resulted in a GIS based map of the area showing the physiognomic type boundaries.

Descriptions were assigned to each physiognomic type based on textural and shading differences of the aerial photographs. The borders of the riverine vegetation on the banks of the Makhutswi River were obvious, as this area was a much darker shade than the surrounding vegetation. Drainage lines were also clearly distinguished as thin 'scars'. These were separated into two types (closed and open drainage lines) based on their shade on the aerial photographs. Grasslands were a light shade and did not contain any trees (dark spots). Wooded grasslands were also a light shade but dotted with trees. The other physiognomic types distinguished in the Conservancy were closed bush with shrubs, open bush with shrubs, closed bush with tall trees and open bush with tall trees. Closed bush had a relatively uniform texture, while open bush did not appear as smooth in texture. Within these two physiognomic types, those that were dotted with dark spots were said to contain tall trees, while those that had a uniform colour, were assigned to the shrub category.

The physiognomic map was ground-truthed to determine the exact position of specific physiognomic boundaries and to ensure that the descriptions that had been assigned to the different patches were consistent throughout the Conservancy. This involved driving, with a hard-copy map of the physiognomic types, to boundaries that could be clearly distinguished (edge of grasslands, drainage lines, open and closed woodlands) and taking GPS readings of these boundaries. The boundaries selected were distributed throughout the Conservancy. Areas

were also checked to ensure that the physiognomic descriptions that they had been assigned were accurate. Ground-truthing also involved mapping areas that contained an abundance of *Colophospermum mopane* trees, areas that had undergone bush clearing and determining where physiognomic types had changed since the aerial photographs had been taken in 1997. When the boundaries of these areas were roads they were included on the physiognomic map by on-screen digitising using the road map or on other occasions a GPS (Garmin 12XL) was used in the field to plot the edges of these areas and then downloaded onto the computer and incorporated in the physiognomic map.

In order to determine the exact densities and species composition within each physiognomic type and to separate each type into vegetation types, 294 transects were sampled throughout the Greater Makalali Conservancy. Only woody plants were sampled in these transects. Although sampling grasses may have provided greater definition within the areas classified as grasslands, the extra time that would have been required to sample the same number of transects throughout the Conservancy would have reduced the efficiency of this method. Mapping the herbaceous layer at such a large scale is also difficult to do (Goodman, 1990) and would not have provided much more clarity in describing the vegetation types.

Three different sets of transects were sampled, although the data collected was the same for each. Each transect was 50m long and their width either 1m or 10m. The one set involved the use of a regular sampling strategy, whereby the entire Conservancy was sampled on a grid system with grid lines 2km apart and a 50m transect every 250m. This grid system was used as the vegetation sampling was undertaken in conjunction with another study to assess elephant utilisation in the Conservancy. 233 transects were sampled in this way between December 1998 and February 1999. Because a regular sampling strategy was used for these transects, some transects may have crossed physiognomic boundaries. However, all physiognomic types within the Conservancy were sampled in these transects. Within these transects, which were 1m wide, measurements of every woody plant species were taken. Transects of the same dimensions were also sampled at 45 sites used for invertebrate sampling (see Chapter Three). These transects were habitat specific, with the result that there were no areas of unique vegetation that were not sampled. A further 16 transects were carried out at approximately 1km intervals in the riverine vegetation along the banks of the Makhutswi River. These transects were set up parallel to the river and were 50m long and 10m wide in order to adequately sample the greater plant diversity. The position of all transects used in the analysis is given in Figure 2.1. This position (located

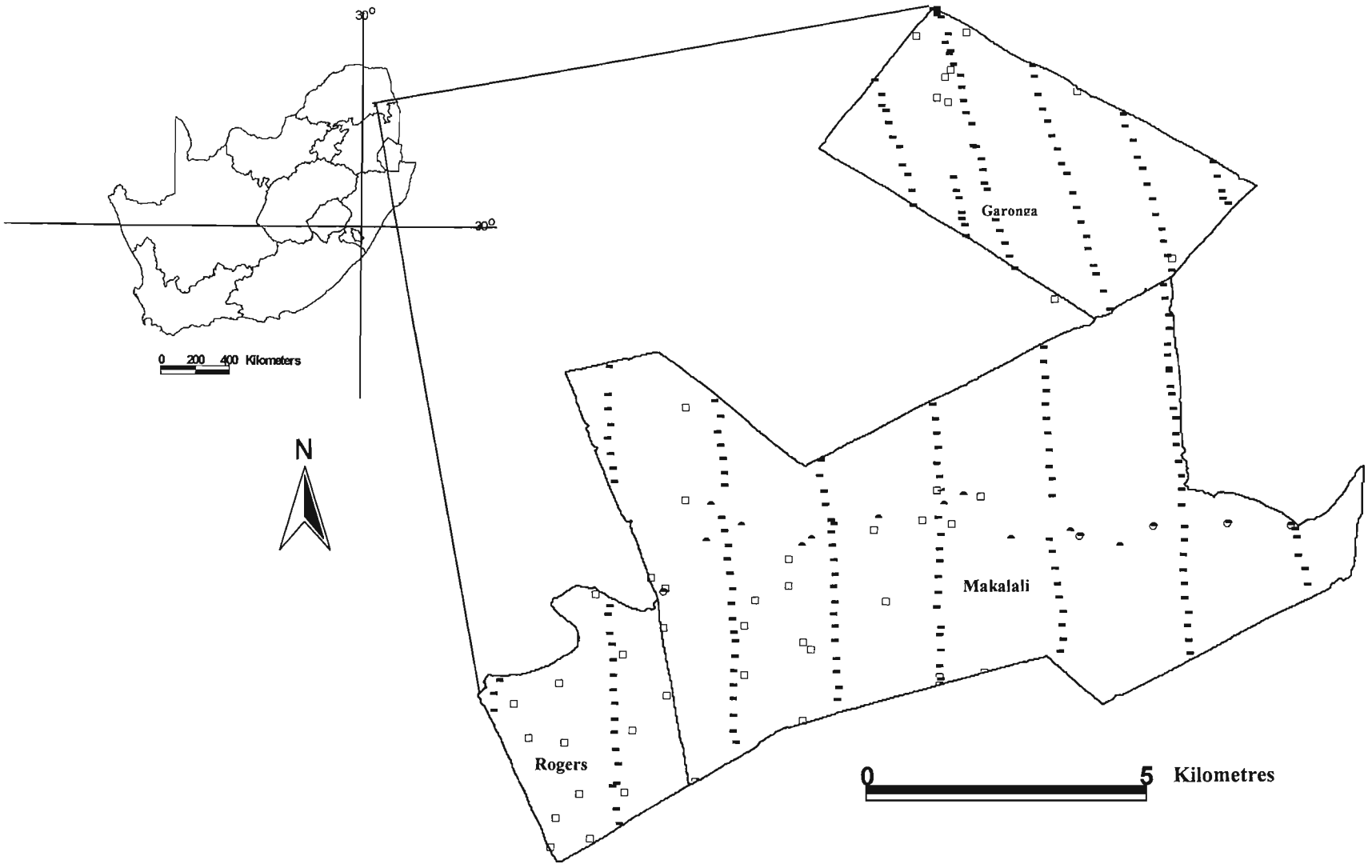


Figure 2.1. The position of the transects used in TWINSPAN to determine the plant communities. Transects carried out from the northern to southern fencelines are represented by black squares, the transects sampled at each of the 45 invertebrate sample sites are white squares, while the riverine transects are indicated by black dots. The position of three of the properties making up the Greater Makalali Conservancy is also shown. The diameter of the symbols is equivalent to approximately 150m. Inset shows the location of the Greater Makalali Conservancy in South Africa.

using a Garmin 12 GPS without differential correction, datum WGS 84) was taken at the centre of each transect.

Within each transect, height, diameter, number of stems and the species of each plant were noted as well as the distance on the transect. All species were identified in the field using the field guides of van Wyk & van Wyk (1997) and Pooley (1994). The *Grewia* species were not identified as separate species because of the difficulty in correctly identifying some of the species due to their potential to hybridise. The heights of the trees below two metres were measured, while the heights of those trees taller than two metres were estimated. The diameters of all trees were measured at approximately 10cm above the soil surface. In the case of multi-stemmed trees, the average diameter of all the stems was recorded. The data were entered into a spreadsheet and then run through a FORTRAN program written by B. Page [1], to calculate density per hectare of each species for each transect.

The resulting density data were then run transferred to the CORNELL format and analysed using Two Way Indicator Species Analysis (Hill, 1994) in the TWINSPAN analysis program. TWINSPAN is a FORTRAN-based computer program designed to show the relationship between a set of samples and the species within those samples as clearly as possible. This is achieved by providing a two-way classification of the data. The samples are classified first using reciprocal averaging with the species classified second using the sample classification as a basis. Differential species are used to split the table. These are species that are preferential to one side of the division. A further ordination is used, that of indicator species. These are the most highly preferential species and are used to refine the ordination procedure (Hill, 1994). The original table, therefore, undergoes various splits, with the first split separating the samples and species that are least closely related. Each of the two remaining groups are then split again, so that the end result is a number of groupings which may relate to different vegetation types.

Various parameters need to be specified in the TWINSPAN analysis. In the analysis that was run on the Conservancy data, most parameters were set to the default, although some were changed. One of the changed parameters was the cut levels. Cut levels relate to the various densities of each species within each sample and are usually set to reflect typical abundance (Hill, 1994). Table 2.1 shows the cut levels that were chosen for these samples.

---

[1] B. Page, Ecologist, School of Life & Environmental Sciences, University of Natal Durban, 4041, South Africa

Table 2.1. The range in density (trees per hectare) used for each cut level in the TWINSPAN analysis

Cut level	1	2	3	4	5	6
Density per ha	0-200	200-600	600-1000	1000-1600	1600-2200	2200-2800

The TWINSPAN analysis is an iterative process. The data need to be run a number of times through the program, each time omitting certain species or transects or changing some of the program parameters. Some transects (samples) or species are not diagnostic and may play a confounding role in the analysis, with the result that clear divisions between plant communities will not be produced. By removing such 'generalist' species and or plots in an iterative process, one is able to select those samples and species that provide the best or distinctive description of the environment.

During each iteration, all the parameters that have already been mentioned were set the same. In the initial analysis all species and all transects (samples) were used. After the first iteration, the *Grewia* species were excluded from use as potential indicators as they occurred in almost every sample and were relatively abundant within these samples. Some transects were also omitted as they occurred on the ecotone between two vegetation communities. Because a regular sampling strategy was used for some of the transects, the transects were not placed within a certain vegetation type, with the result that some of the transects occurred on ecotone boundaries. The final analysis was run with 285 samples and 81 plant species.

Once a Two Way Indicator Species Analysis had been carried out on the density data, the physiognomic types were reclassified on the basis of the species and sample sites classification. However, in some instances, TWINSPAN identified two separate plant communities within one physiognomic type. In these cases, the final vegetation map comprised a combination of two TWINSPAN plant communities.

In this analysis, when TWINSPAN splits the samples, it splits each group until it reaches the number of levels that were specified with the other parameters at the beginning of the analysis or until a minimum of five samples are left in the group. This results in the final analysis containing groups of samples that are split further than what could be considered a meaningful community type. One, therefore, needs to decide at what split level of the TWINSPAN classification to assign a vegetation community.

In order to describe the exact species composition, density and structure within a vegetation group, all the transects that occurred within the same community, sub-community or variant were grouped together and run through a FORTRAN population structure computer program written by B. Page. This program determined the species composition and the density of each species in seven height classes (Table 2.2) for each vegetation type. These results were used to generate the final description for each vegetation type.

Table 2.2. The seven height classes used in the FORTRAN population structure program.

Size class	1	2	3	4	5	6	7
Height range (m)	0-0.5	0.5-1.5	1.5-3	3-5	5-8	8-12	12-30

The Edwards (1983) system of classification for vegetation in southern Africa was used to classify each vegetation type according to a common classification system. This structural classification system is based on a set of four growth forms, four cover classes and a set of four height classes for each growth form (Edwards, 1983). The four growth forms include trees, shrubs, grasses and herbs. For this study grasses and herbs were not sampled and as a result are not discussed. Edwards (1983) describes trees as being rooted, woody, self-supporting plants over 2m high and with one or a few definite trunks normally branching above ground level, while shrubs are rooted, woody, self-supporting plants up to 5m tall, multi-stemmed and branching at or near ground-level when 2m to 5m tall, or either multi-stemmed or single stemmed when less than two metres tall.

The FORTRAN population structure program used 1.5m as a cut off for the second height class. As a result, instead of using 2m as the cut-off for shrubs, all woody plants under 1.5m tall were considered shrubs, while those woody plants over 1.5m but under 5m that are usually multi-stemmed were also considered shrubs. The plants that fell into this category were *Dichrostachys cinerea*, *Cissus cornifolia*, *Euclea divinorum*, *Euclea natalensis*, *Flueggea virosa*, *Gymnosporia buxifolia*, *Terminalia prunioides*, *Nuxia oppositifolia* and *Strychnos madagascariensis*. All those woody plants over 5m tall were considered trees, while those species other than those mentioned above between the heights of 1.5m and 5m were also considered to be trees.

The cover that is referred to in Edwards' (1983) vegetation classification system is the projected crown cover and is determined by calculating the total canopy cover (out of 100%) of each growth form (Edwards, 1983). In order to determine the final percentage canopy cover of both shrubs and trees and to determine to which cover class each vegetation community belonged, an approximate percentage canopy cover was determined from aerial photographs. This was used

in conjunction with the results from the TWINSPAN analysis (percentage tree and shrub cover) to assign each vegetation community to a structural group.

Development of maps of soil variables

Soil samples were collected at 68 sites (see Figure 2.2) throughout the Greater Makalali Conservancy. Forty five sites were located at the invertebrate sample sites, while the others were located in areas between these sites, in order to give a relatively good coverage of the areas around the sample sites. The soil was collected by digging to a depth of approximately 15cm using a hand trowel and then removing the soil that occurred from the surface to that depth and placing it in a soil sample box (6 x 8.5 x 9cm). Enough soil was collected at each site to fill one box. These samples were taken to Cedara Agricultural College, Kwa-Zulu Natal for analysis. During these analyses, agriculturally important soil variables including bulk density, zinc concentration, manganese concentration, soil exchange acidity, total cations, pH and clay percentage were determined.

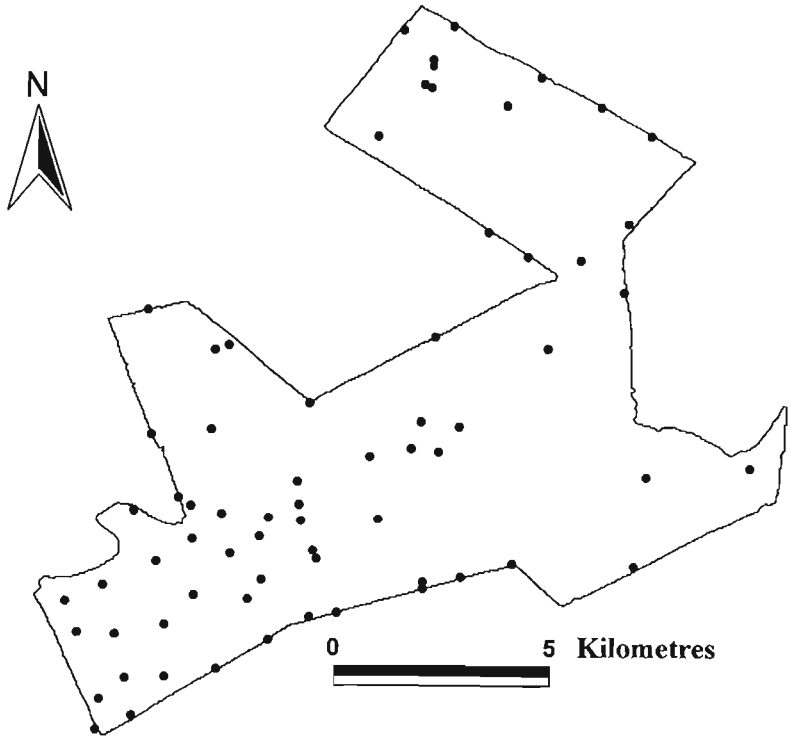


Figure 2.2. Distribution of the 68 soil sample sites in the Greater Makalali Conservancy.

In order to create maps of each of these variables over the whole Conservancy, the values were interpolated in ArcView. The interpolation function generates a surface over the whole area

under study, from a set of points using nearest neighbour analysis. All 68 soil sample points were used to create maps of each of the soil variables mentioned above.

Development of soil surface temperature map

An interpolated map of relative soil surface temperature was also created for the Conservancy. Sites throughout the Conservancy were used to measure invertebrate diversity during three sampling periods. During each sampling period 15 sites were sampled, with the result that 45 sites were sampled at various times during the study. During each of these periods the minimum and maximum temperatures of the upper 0.75cm of soil over a one week period was recorded at the 15 sites being sampled during that period. Soil temperatures were, therefore, recorded at 15 sites from the end of February to mid March 1999, at 15 sites from early to mid November 1999 and at a further 15 sites from late February to the end of February 2000. In order to factor out any effect that sampling period may have on temperature, an ANOVA was run with soil temperature as the dependant variable and sample period as the independent variable. The residuals were saved and used as the values with which the interpolated map was created.

At each site a maximum/minimum thermometer was buried horizontally under a thin layer (0.75cm) of soil, at each site, in an area where the soil above the thermometer would receive maximum sunlight during the day. The amount of soil used to bury the thermometer was just enough to cover its surface. The thermometers measured the minimum and maximum temperature of the soil covering them over a one week period.

Development of air temperature map

During the same sampling periods that soil temperature was recorded at each of the 45 sampling sites, so was air temperature. Minimum/maximum thermometers were set up at each site to record the minimum and maximum air temperature over a one week period. These thermometers were tied to the stem of a tree, at a height of approximately 1.5m above the ground. Each thermometer was set up on the southern side of the tree in a position where they would receive little or no direct sunlight during the course of the day. As with the thermometers that measured soil temperature, thermometers were only set up at the sites that were being sampled during the particular sampling period. These thermometers were set up from late February to the end of February 1999, the end of October to early November 1999 and mid February to late February 2000. In order to factor out any possible effect that sample period may

have had on the temperatures recorded, an ANOVA was run using the mean of the minimum and maximum temperatures recorded at each site as the dependant variable and sample period as the independent variable. The residuals were saved and then interpolated from all 45 sites, to produce a map of relative air temperature over the Conservancy.

Development of the rainfall map

In order to produce a map showing variation in rainfall over the Greater Makalali Conservancy, 11 rain gauges were set up at various points in the Conservancy. After each rainfall event the rainfall collected in each of these rain gauges was collected and recorded by Conservancy staff. Rainfall data was collected from 8 January 1999 to 12 November 2000. In order to determine the average rainfall per rainfall event at each of the 11 sites over this almost 2 year period, the readings at each site were totalled and averaged by dividing by the number of rainfall events. These average values were then interpolated in ArcView from the 11 recording points to produce a map of average rainfall over the Conservancy.

Altitude variables

Altitude was determined using a GIS-based Digital Elevation Model (DEM) of the Greater Makalali Conservancy. 1:50 000 height contours (20m height intervals) were obtained from the Surveyor General in South Africa as a GIS image. Frank Sokolic[2] converted these contours to a DEM, with a 20m grid. The contours were in Latitude/Longitude degrees and were re-projected to the South African LO coordinate system in meters. The coordinates making up the contours were then used as input into a program called Surfer. Surfer generates regular grids from irregularly spaced point data. The Kriging gridding method was used to generate the DEM with a cell size of 20m by 20m. The resulting 20m grid was exported from Surfer in ASCII format and imported into the ArcView GIS program as a grid using the Spatial Analyst extension.

Using the DEM and the 'Derive Aspect' and Derive Slope' functions in ArcView, aspect (metres) and slope maps (degrees) were created for the Conservancy.

[2] Frank Sokolic, School of Life and Environmental Sciences, University of Natal Durban, 4041, South Africa

Results

Vegetation map

The physiognomic map (Figure 2.3) was created using visual differences seen on aerial photographs. However, in some cases what initially appeared to be different habitats were later assigned to the same vegetation community in the final vegetation map of the Conservancy (Figure 2.4).

The full output table for the TWINSPAN analysis is presented in Appendix A. This divisions at the bottom of the appendix show where the splits between the various communities, sub-communities and variants occurred in the analysis. The first community to be separated out was the *Colophospermum mopane* low closed woodland, with the riperian and drainage-line low closed woodlands being separated from the other vegetation communities next. Although the *Cissus cornifolia – Commiphora africana* low thicket was separated in the TWINSPAN analysis as a sub-community of the *Combretum apiculatum – Acacia nigrescens* woodland, it was kept as a separate community as it contained a low density of the medium to large trees such as *Acacia nigrescens*, *Combretum hereroense* and *Sclerocarya birrea* and a larger density of some of the smaller species such as *Cissus cornifolia* and *Commiphora africana*.

The TWINSPAN analysis produced a total of 11 vegetation communities, sub-communities and variants within these sub-communities. However, some physiognomic types contained equal numbers of two groups of sites as identified by TWINSPAN. As a result, these areas were assigned to separate vegetation types, which contained a combination of these two groups identified by TWINSPAN. The final vegetation map took into consideration those physiognomic types that contained these two groups of sites as identified by TWINSPAN and therefore, contained a total of 16 vegetation types, subgroups and variants, some of which would not have been shown on the TWINSPAN output table. Rocky outcrops were also described as a separate vegetation type, even though their vegetation composition, in many cases, would be very similar to or exactly the same as that of the surrounding vegetation. Rocky outcrops were separated as their surface structure is different to the surrounding areas and as a result would serve as a different micro-habitat for small organisms such as small mammals and certain invertebrate groups.

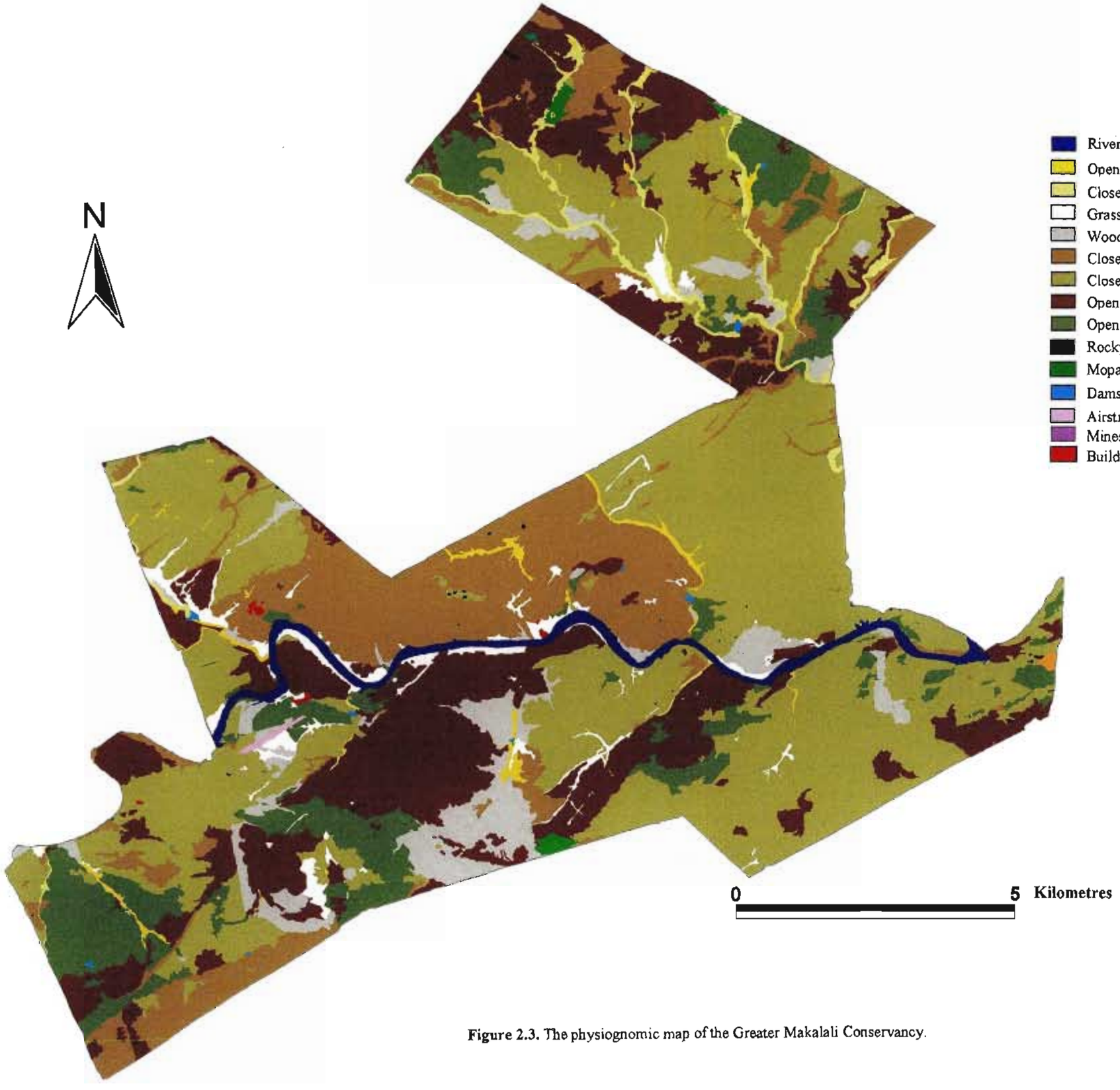


Figure 2.3. The physiognomic map of the Greater Makalali Conservancy.

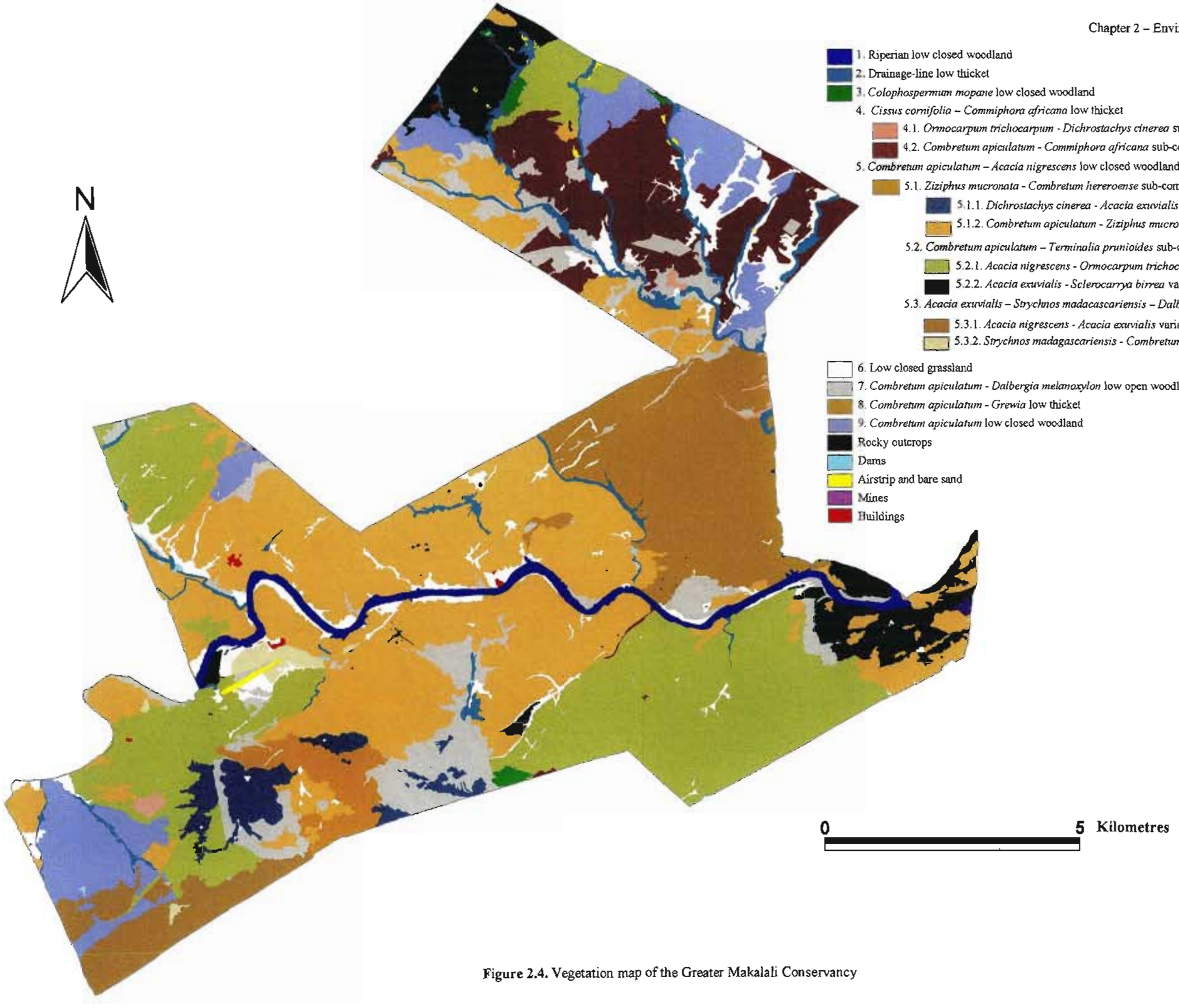


Figure 2.4. Vegetation map of the Greater Makalali Conservancy

The maps of all the soil variables (Figures 2.5 to 2.11) show that although the range in many of the factors was not large, there was variation throughout the Conservancy. However, although there was variation, the values for most of the variables in the south western corner of the Conservancy were consistently different to those in the rest of the Conservancy. The soil in this area is visually different, being much whiter and coarser than soil in the rest of the Conservancy. Both relative soil (Figure 2.12) and air temperatures (Figure 2.13) also varied throughout the Conservancy, although their range was also fairly small. The rainfall map (Figure 2.14) was created using the average amount of rain that fell at each recording site during each rainfall event. As the recording station on the north eastern side of the Conservancy receives the highest average rainfall, it appears as if the rainfall may be higher in the north eastern section and decrease from east to west across the Conservancy.

The altitude map (Figure 2.15) shows that the highest point on the Conservancy is against the northern fenceline in Garonga, while the Makhutswi River flows from west to east through the lowest sections of the Conservancy. As the altitude decreases from both the northern and southern fences towards the Makhutswi River, most of the area south of the river has north facing slopes, while most of the area north of the river is south facing (Figure 2.16). Figure 2.17 shows that much of the Conservancy is relatively flat, with a slope of 0 to 6 degrees. Steepest slopes occur in its eastern corner, where there is an old mica mine.

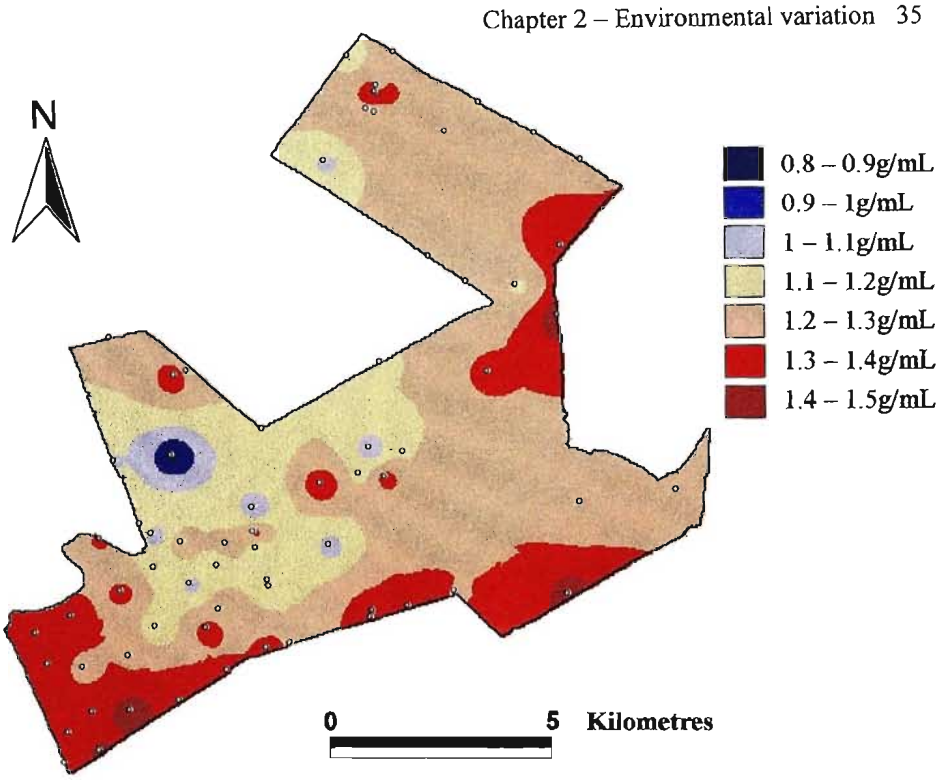


Figure 2.5. Soil density of the Greater Makalali Conservancy. The map was created by interpolation from 68 sample points (white dots).

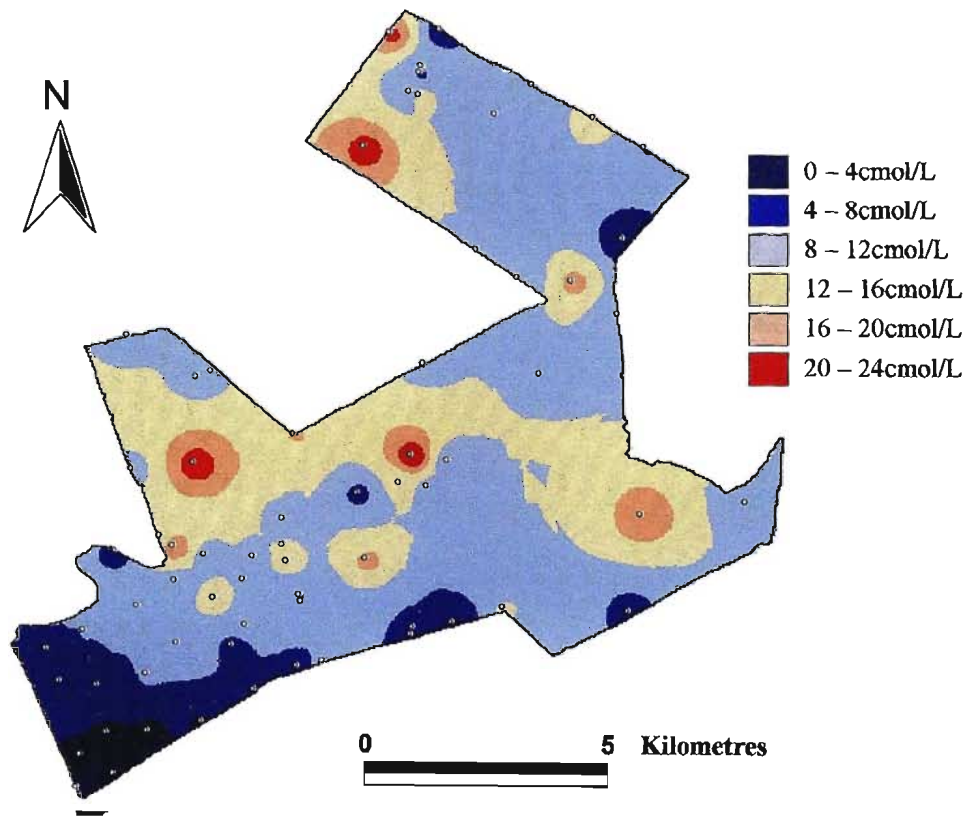


Figure 2.6. Total soil cations of the Greater Makalali Conservancy. The map was created by interpolation from 68 sample points (white dots).

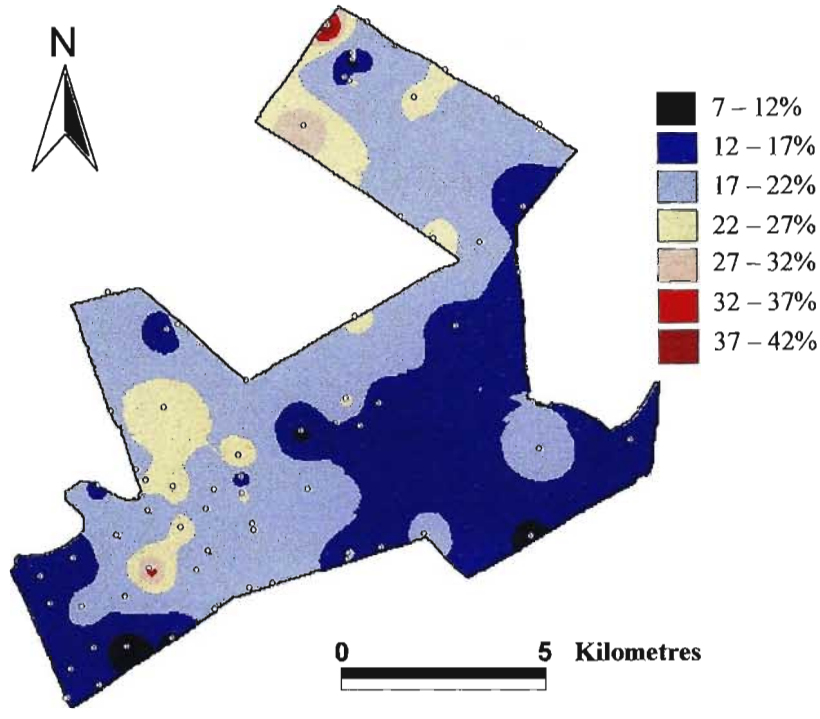


Figure 2.7. Soil clay percentages of the Greater Makalali Conservancy. The map was created by interpolation from 68 sample points (white dots).

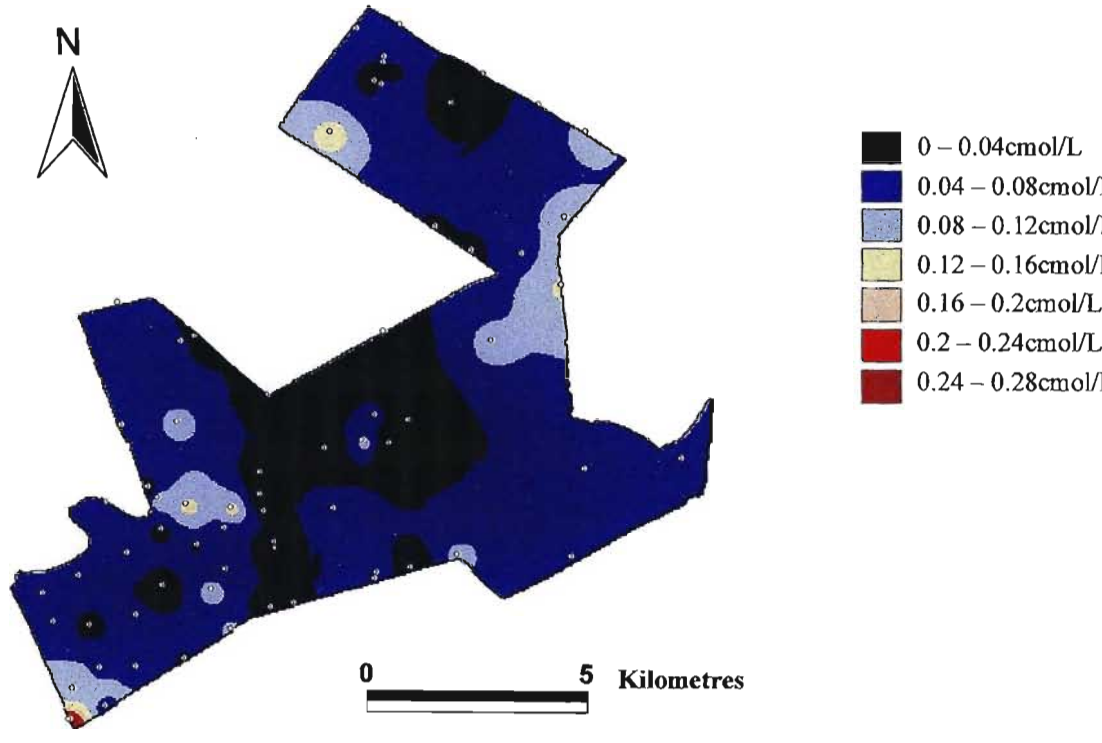


Figure 2.8. Soil exchange acidity of the Greater Makalali Conservancy. The map was created by interpolation from 68 sample points (white dots).

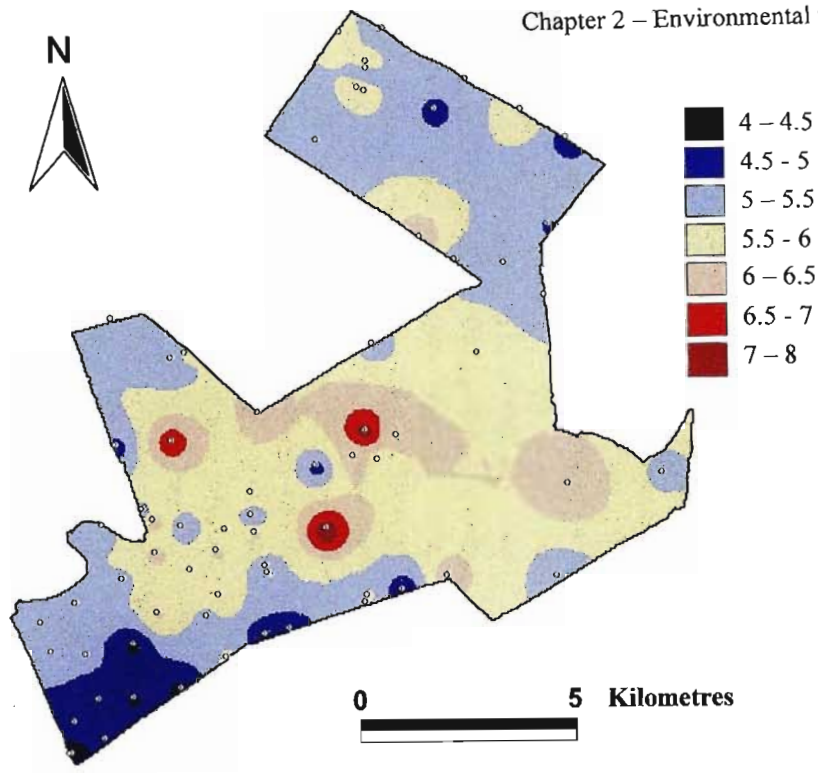


Figure 2.9. Soil pH of the Greater Makalali Conservancy. The map was created by interpolation from 68 sample sites (white dots).

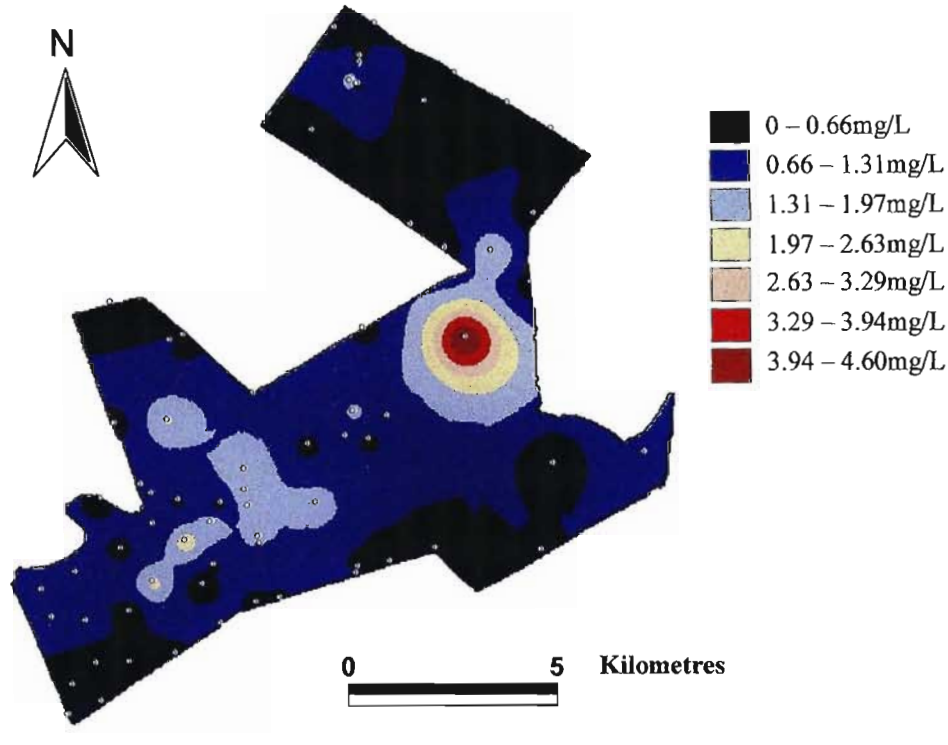


Figure 2.10. Soil zinc content of the Greater Makalali Conservancy. The map was created by interpolation from 68 sample sites (white dots).

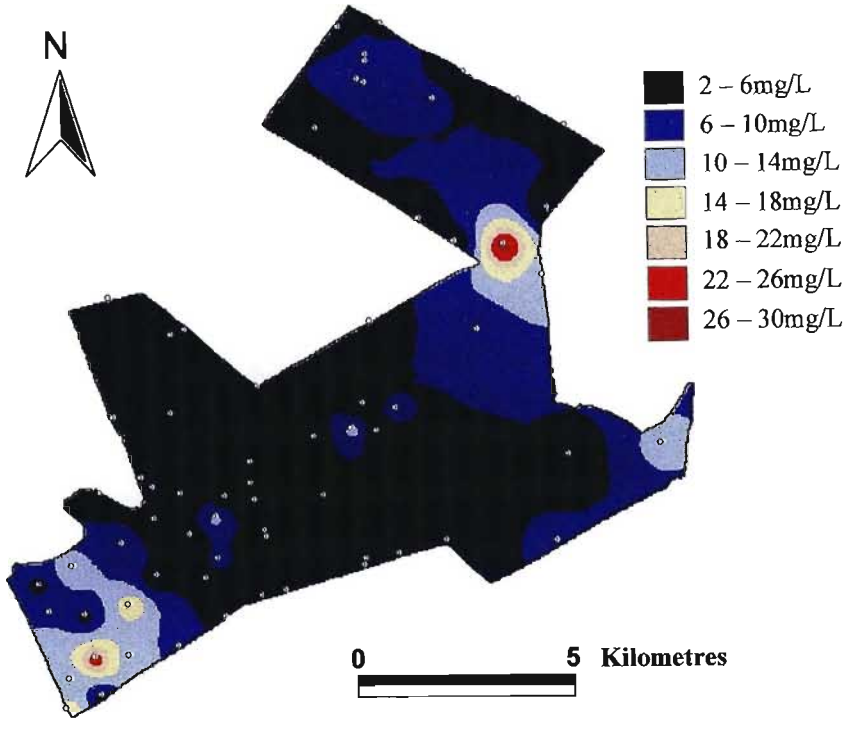


Figure 2.11. Soil magnesium content of the Greater Makalali Conservancy. The map was created by interpolation from 68 sample points (white dots).

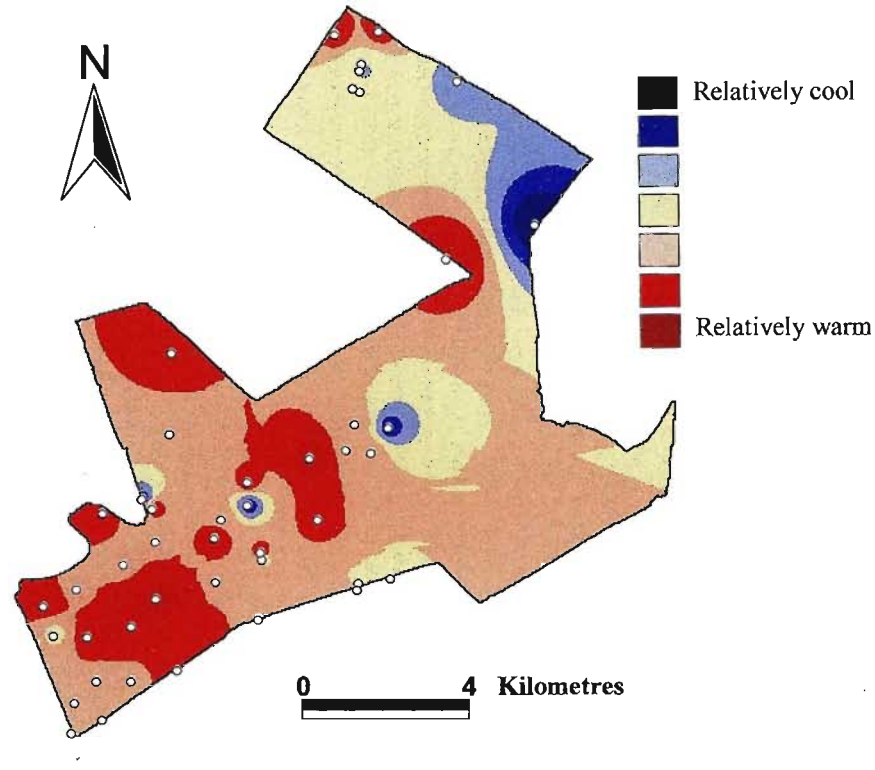


Figure 2.12. Variation in relative soil temperature in the Greater Makalali Conservancy. The map was created by interpolation from 45 sample points (white dots). Temperatures ranged from 28.5 to 36.5°C.

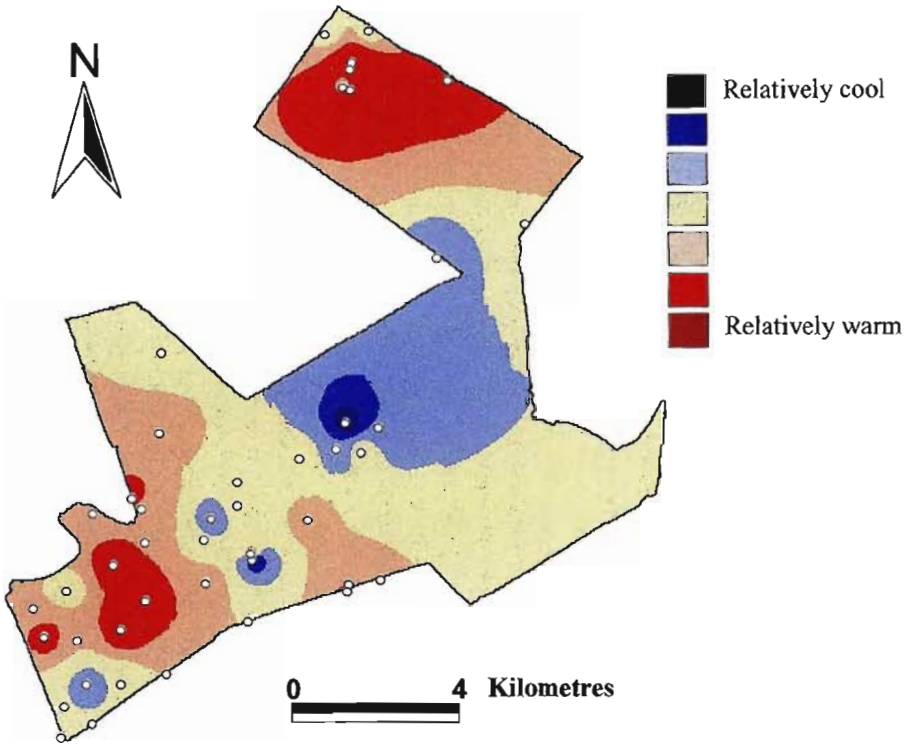


Figure 2.13. Variation in relative air temperature in the Greater Makalali Conservancy. The map was created by interpolation from 45 sample points (white dots). Temperatures ranged from 24 to 32°C.

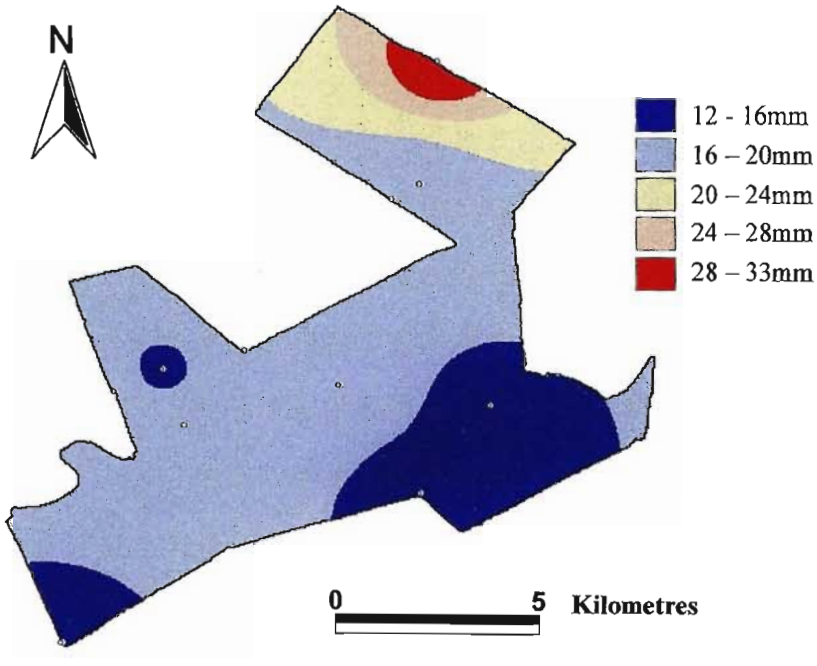


Figure 2.14. Average rainfall per rainfall event for the Greater Makalali Conservancy. The map was created by interpolation from 11 recording stations (white dots).

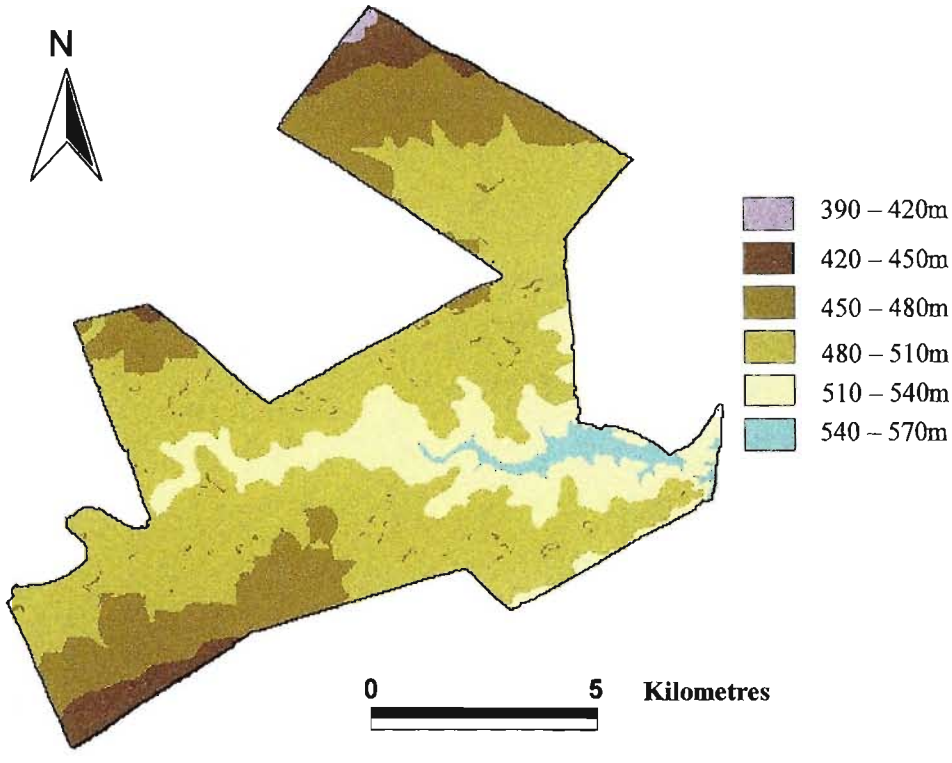


Figure 2.15. Altitude of the Greater Makalali Conservancy. The Makhutswi River flows from west to east through the areas of lowest altitude.

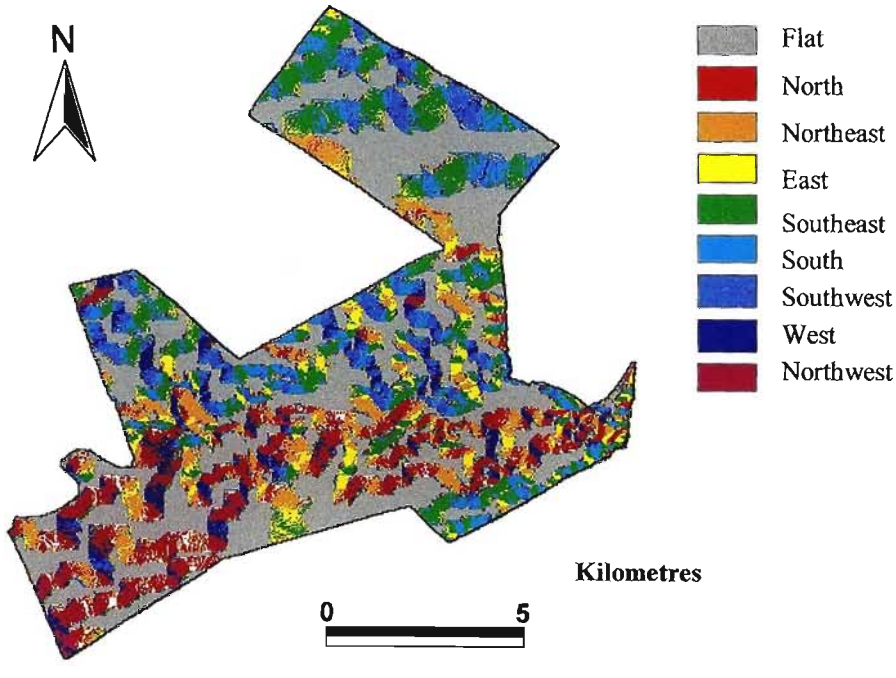


Figure 2.16. Aspect of the Greater Makalali Conservancy.

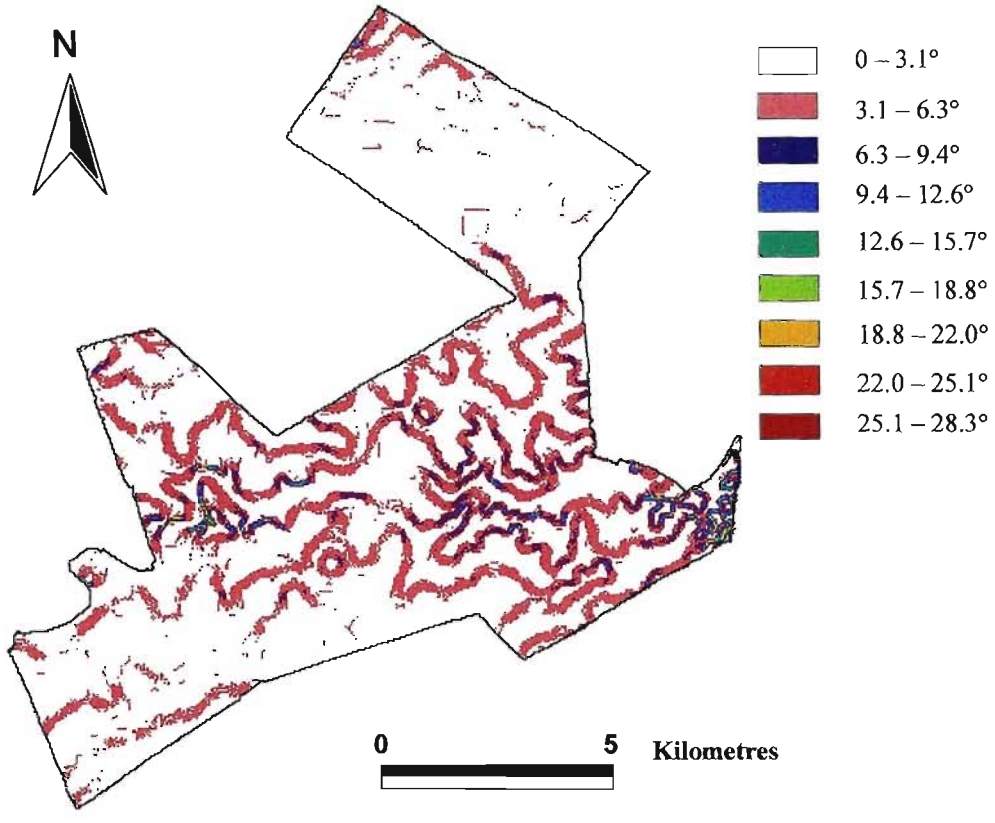


Figure 2.17. Slope of the Greater Makalali Conservancy. The steepest slopes in the eastern corner are associated with an old mica mining area.

The descriptions of each vegetation type are given below. The vegetation names were assigned using structural groups based on Edwards' system of vegetation classification for southern Africa and characterising species as determined by the TWINSPAN analysis. Where there were more than two characteristic species, the two most abundant were used.

The vegetation types were described using the results of the TWINSPAN analysis, the results of the density analysis carried out by B. Page as well as a summary of the environmental characteristics for each vegetation type (Table 2.3). This summary contains the mean value, per vegetation type, of each environmental variable mapped. In order to obtain these values, the Summarize Zones function in ArcView was used. These were also used in the description of the vegetation types. Names were assigned to the vegetation types using the two species that distinguished the vegetation type most, as opposed to species that were the most abundant. Using the results of the TWINSPAN analysis Table 2.4 was produced, which shows the relative abundance of all species recorded within each plant community.

Table 2.3. Summary of the characteristics of the vegetation types in the Greater Makalali Conservancy.

	Rainfall (mm)	Height (m)	Aspect	Slope (°)	Soil density (g/ml)	Exchange acidity (cmol/L)	Total cations (cmol/L)	pH	Mn (mg/L)	Zn (mg/L)	Soil clay (%)
1. Riperian low closed woodland	16.7	431	E	2.5	1.20	0.059	13.3	5.93	5.3	1.05	18.5
2. Drainage-line low thicket	19.5	474	NE	0.9	1.24	0.066	11.7	5.53	6.8	0.85	19.7
3. *Colophospermum mopane* low closed woodland	21.0	492	E	0.7	1.32	0.057	8.6	5.40	6.1	0.90	16.1
4.1. *Ormocarpum tricocarpum - Dichrostachys cinerea* low thicket	17.4	469	S	1.5	1.32	0.077	9.3	5.30	10.6	0.86	17.4
4.2. *Combretum apiculatum - Commiphora africana* low thicket	21.4	482	E	0.8	1.27	0.062	10.5	5.34	6.4	0.62	19.7
5.1. *Ziziphus mucronata - Combretum hereroense* low closed woodland	17.1	491	E	1.1	1.23	0.054	9.3	5.42	5.0	1.01	19.4
5.1.1. *Dichrostachys cinerea - Acacia exuvialis* low closed woodland	16.9	483	E	1.1	1.23	0.056	9.5	5.47	5.8	1.08	21.6
5.1.2. *Combretum apiculatum - Ziziphus mucronata* low closed woodland	17.3	464	E	2.4	1.20	0.055	12.8	5.80	5.4	1.04	19.2
5.2.1. *Acacia nigrescens - Ormocarpum tricocarpum* low closed woodland	16.5	471	SE	2.0	1.28	0.066	10.7	5.62	5.7	0.70	17.2
5.2.2. *Acacia exuvialis - Sclerocarrya birrea* low closed woodland	19.1	474	SE	3.3	1.26	0.066	12.6	5.67	6.9	0.87	18.8
5.3.1. *Acacia nigrescens - Acacia exuvialis* low closed woodland	18.1	471	S	3.1	1.21	0.087	11.5	5.51	5.3	1.00	20.3
5.3.2. *Strychnos madagascariensis - Combretum apiculatum* low closed woodland	15.7	514	SE	1.3	1.37	0.088	4.1	4.73	12.0	0.52	13.2
6. Low closed grassland	18.4	462	E	1.3	1.24	0.066	11.4	5.59	5.7	0.84	18.4
7. *Combretum apiculatum - Dalbergia melanoxylon* low open woodland	17.4	474	E	1.3	1.23	0.066	11.7	5.60	5.8	0.87	19.9
8. *Combretum apiculatum – Grewia* low thicket	20.3	488	SE	1.3	1.29	0.065	9.1	5.23	7.8	0.68	17.8
9. *Combretum apiculatum* low closed woodland	16.8	459	E	2.3	1.28	0.074	12.0	5.74	8.4	1.94	17.0
10. Rocky outcrops	18.5	472	SE	5.3	1.23	0.055	12.3	5.68	6.3	1.01	19.7

Note: The values presented are means of all values recorded in each vegetation type.

Table 2.4. Table of all species sampled in the vegetation transects, showing their relative abundance in each vegetation type. A = abundant, C = common, R = rare and a dash indicates absence. The numbers referring to the vegetation types match those given in the text.

	1	2	3	4.1	4.2	5.1.1	5.1.2	5.2.1	5.2.2	5.3.1	5.3.2	6	7	8	9
Acacia burkei	-	-	-	R	-	-	-	-	-	-	-	-	-	-	-
Acacia caffra	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Acacia exuvialis	R	R	R	R	C	C	R	R	C	A	C	R	R	R	R
Acacia gerradii	R	-	-	-	-	-	R	R	-	-	-	-	-	-	-
Acacia karroo	-	R	-	-	-	-	R	R	-	-	-	-	R	R	-
Acacia tortilis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Acacia nigrescens	C	R	R	C	R	C	A	C	C	C	R	C	R	R	C
Acacia nilotica	R	R	R	-	-	R	R	R	R	R	-	-	R	R	-
Acacia polycantha	R	-	-	-	-	R	-	-	-	-	-	-	-	-	-
Acacia robusta	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Acacia schweinfurthii	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Albizia harveyi	C	R	-	R	R	R	-	-	-	R	-	-	R	R	-
Albizia species	-	R	-	R	R	-	R	R	R	-	-	-	-	R	-
Balanites maughamii	R	-	-	-	-	R	R	-	-	-	C	-	-	R	-
Berchemia discolor	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Berchemia zeyheri	R	-	-	-	-	-	-	R	R	-	-	-	-	-	-
Bolusanthus speciosus	-	R	-	-	R	-	R	R	R	-	-	-	R	-	-
Boscia albitrunca	-	-	-	-	-	-	R	R	-	-	-	R	-	-	-
Bridelia mollis	R	-	-	-	-	-	R	R	-	-	-	-	-	-	-
Canthium ciliatum	-	-	-	R	-	-	R	-	-	-	-	-	-	-	-
Carissa bispinosa	-	-	-	R	-	-	-	-	-	-	-	-	-	-	-
Cassine transvaalensis	R	R	-	R	R	-	-	-	-	-	-	-	-	-	-
Cissus cornifolia	-	-	-	R	C	R	R	R	R	-	R	-	R	R	-
Clausena anisata	-	-	-	-	-	-	-	-	R	-	-	-	-	-	-
Colophospermum mopane	-	-	A	-	-	-	-	-	-	-	-	-	-	-	-
Combretum apiculatum	C	-	C	C	A	R	A	A	A	C	C	C	R	C	A
Combretum erythrophylum	C	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Combretum hereroense	R	-	R	R	R	C	C	R	R	R	R	R	R	R	C
Combretum imberbe	C	R	R	-	R	-	R	R	-	-	-	-	R	R	R
Combretum molle	R	-	-	-	-	-	-	R	-	-	-	-	-	-	-
Combretum zeyheri	-	-	-	-	-	-	-	R	-	-	C	-	-	R	-
Commiphora africana	-	-	-	-	C	-	R	R	R	R	R	R	R	C	R
Commiphora glandulosa	-	R	-	C	R	R	R	R	R	R	-	-	-	R	R
Commiphora mollis	-	-	-	-	-	-	R	R	R	-	-	R	-	-	-
Commiphora schimperi	-	-	-	-	-	-	-	R	-	-	-	-	-	-	-
Croton megalobotrys	A	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dalbergia melanoxylon	R	C	C	R	R	-	R	R	-	R	-	R	R	R	-
Dichrostachys cinerea	A	-	C	C	R	C	C	C	R	R	C	R	R	R	R
Diospyros mespiliformis	A	-	-	R	R	-	R	-	R	-	-	-	R	-	-
Dombeya rotundifolia	R	-	R	R	-	-	R	R	-	-	-	-	-	R	-
Ehretia amoena	R	-	-	R	R	-	R	R	-	-	-	-	R	R	R
Ehretia rigida	R	C	R	-	-	-	-	-	-	-	-	-	-	-	-
Euclea crispa	R	-	-	-	-	-	-	-	-	-	-	-	R	-	-
Euclea divinorum	R	R	C	-	R	R	R	R	-	-	-	-	R	R	-
Euclea natalensis	C	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Euphorbia species	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ficus capreifolia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ficus ingens	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ficus sycamorus	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Flueggea virosa	A	R	-	R	R	-	R	R	R	-	-	R	R	R	R
Gardenia volkensii	R	-	-	R	-	-	-	-	-	-	-	-	-	-	-
Gossypium herbaceum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Grewia species	A	A	A	A	A	A	C	C	C	R	-	A	A	C	C
Gymnosporia buxifolia	A	A	R	R	R	R	R	R	R	-	-	-	R	R	R
Gymnosporia senegalensis	-	-	-	R	R	-	-	-	-	-	-	-	R	-	-
Kirkia wilmsii	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lannea schweinfurthii	-	C	-	R	C	-	R	-	-	-	-	-	R	R	R
Lonchocarpus capassa	C	C	-	R	R	-	R	R	R	R	-	-	R	R	R
Mimusops zeyheri	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nuxia oppositifolia	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ormocarpum trichocarpum	R	-	-	C	R	-	R	R	-	R	-	R	R	R	R
Ozoroa paniculosa	-	-	-	-	-	-	R	R	R	-	-	-	-	-	-
Pappea capensis	C	-	-	-	R	-	-	R	-	-	-	-	-	-	-
Peltophorum africanum	-	R	-	-	-	-	R	R	-	-	-	-	-	R	R
Phoenix reclinata	C	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pterocarpus rotundifolius	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rhoicissus tridentata	-	-	-	R	-	-	-	-	-	-	-	-	-	-	-
Rhus rehmanniana	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sclerocarrya birrea	C	-	R	-	R	-	C	R	C	R	-	R	-	R	C
Scotia brachypetala	R	-	-	-	-	-	R	R	R	-	-	-	-	-	-
Spirostachys africana	R	R	R	C	R	R	R	-	-	-	-	-	R	-	-
Sterculia rogersii	-	-	-	-	-	-	R	-	-	-	-	R	-	-	-
Strychnos madagascariensis	-	R	-	R	-	-	R	R	-	R	A	-	R	R	-
Tecomaria capensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Terminalia prunioides	C	-	R	-	R	R	-	R	C	R	-	R	-	R	R
Terminalia sericea	-	-	-	-	-	-	-	-	-	R	-	-	-	-	-
Ximenia americana	R	-	R	-	-	-	-	-	-	-	-	-	-	-	-
Ximenia caffra	-	-	-	-	-	-	-	-	R	R	-	-	-	-	-
Ziziphus mucronata	A	-	-	R	R	C	C	R	-	R	-	R	R	R	R
Unknown species	C	R	-	-	-	-	R	R	-	R	-	-	R	-	-

Note: Rare species occurred in less than 25% of the transects within a vegetation type, common species occurred in 25 – 75% of the transects while abundant species were found in more than 75% of the transects sampled within a vegetation type. *Euphorbia* species refers to a single unidentified species, while *Grewia* species refers to all species from this genus recorded in the Greater Makalali Conservancy.

1. Riperian low closed woodland

This vegetation community is restricted to the banks of the Makhutswi River and ranges in width from approximately 10m to 60m either side of the river. It contains 47 species, the largest variety of woody plant species in a single vegetation community in the Conservancy. This woodland is characterised by *Flueggea virosa*, *Croton megalobotrys*, *Dichrostachys cinerea*, *Ziziphus mucronata* and *Gymnosporia buxifolia*, while *Phoenix reclinata* and *Diospyros mespiliformis* also occur in relatively high densities. There are a number of species that are restricted to this community. They include *Acacia robusta*, *Acacia caffra*, *Acacia schweinfurtheii*, *Berchemia discolor*, *Combretum erythrophylum*, *Euphorbia* sp., *Euclea natalensis*, *Ehretia rigida*, *Ficus sycamorus* and *Ficus ingens*.

Fifteen percent of all the woody plants in this vegetation community were taller than 5m high, while 7% were taller than 8m. The average height of trees taller than 5m was 10.2m. *Combretum hereroense*, *Spirostachys africana*, *Gymnosporia buxifolia* and *Sclerocarya birrea* dominate this height category.

As would be expected, this community occurs in the lowest areas of the Conservancy, at an average elevation of 430m above sea level.

2. Drainage-line low thicket

This vegetation community is found in and along the drainage lines in the Conservancy. Most of these drainage lines are, however, found in the Garonga section to the northeast of the Conservancy. The species that characterise this community are *Albizia harveii*, *Loncocarpus capassa*, *Commiphora glandulosa* and *Flueggea virosa*. *Gymnosporia buxifolia* and *Grewia* species are also abundant in this vegetation community. Although there are some tall trees within this thicket, 88.6% of the woody plants are less than 5m high.

3. *Colophospermum mopane* low closed woodland

This vegetation community is distinguished and dominated by *Colophospermum mopane* trees. This woodland is restricted to a few small, isolated pockets along the southern fenceline in Makalali and Garonga and in the northern section of Garonga. Twenty woody plant species were recorded in the transects undertaken in this community. However, most were probably

only present due to the small size of the patches of this community. Species such as *Grewia* species, *Euclea divinorum*, *Combretum hereroense*, *Commiphora glandulosa*, *Dalbergia melanoxylon* are present in low densities. Although there are a few large *Colophospermum mopane* trees in this woodland, 74% of the woody plants are less than 1.5m tall. There has been heavy utilisation of this vegetation type by elephant (*Loxodonta africana*) which may be a reason for the lack of medium to tall trees. The grass cover in this woodland is fairly sparse, with most of the grasses that do grow in this vegetation type growing, more often than not, at the base of trees other than *Colophospermum mopane*. This community occurs on soils with a lower mean clay content than any other vegetation type.

4. *Cissus cornifolia - Commiphora africana* low thicket

This vegetation community is predominantly found in the Garonga section of the Conservancy, although there are a few small patches in Makalali. The species characterising this community are *Cissus cornifolia*, *Commiphora africana* and *Lannea schweinfurtheii*. Two sub-vegetation types are recognised within this low thicket.

4.1 *Ormocarpum trichocarpum – Dichrostachys cinerea* sub-community

The characterising species in this thicket are *Dichrostachys cinerea*, *Ormocarpum trichocarpum*, *Commiphora glandulosa* and *Combretum hereroense*. There is a low diversity of woody plants within this vegetation type with *Grewia* species, *Dichrostachys cinerea*, *Ormocarpum trichocarpum* and *Commiphora glandulosa* being the most abundant species. Other species recorded in more than one transect include *Combretum hereroense*, *Cissus cornifolia* and *Spirostachys africana*. The shrub species form 81% of the woody species in this thicket, while 33% of all woody plants recorded are less than 1.5m tall.

A relatively high magnesium level is found within this community, while this community is one of only two that is predominantly south facing.

4.2 *Combretum apiculatum - Commiphora africana* sub-community

This low thicket is only found in the Garonga section of the Conservancy. *Grewia* species occupy the highest density of woody plants in this sub-community, although the relatively high densities of *Combretum apiculatum* and *Commiphora africana* distinguish this thicket from the other thickets. Other species that occur in relatively high densities include *Acacia exuvialis, Acacia nigrescens, Dalbergia melanoxylon* and *Lannea schweinfurtheii.*

5. *Combretum apiculatum – Acacia nigrescens* low closed woodland

This is the most prevalent community in the Conservancy. It is found in large areas throughout the Makalali section and in the northern and western areas of the Garonga section and is characterised by *Combretum apiculatum, Acacia nigrescens, Ziziphus mucronata* and *Sclerocarya birrea* species. Three sub-communities, each with two variants are found within this community.

5.1 *Ziziphus mucronata – Combretum hereroense* sub-community

5.1.1 *Dichrostachys cinerea – Acacia exuvialis* variant

The high density of *Acacia exuvialis* and the presence of *Dichrostachys cinerea* characterise this variant. *Acacia nigrescens, Combretum apiculatum* and *Combretum hereroense* are also prevalent, while *Grewia* species and *Commiphora glandulosa* are also present.

5.1.2 *Combretum apiculatum – Ziziphus mucronata* variant

The species characterising this variant are *Combretum apiculatum* and *Ziziphus mucronata.* Other species that occur in high densities are *Acacia nigrescens* and *Grewia* species, while other relatively abundant species include *Combretum hereroense* and *Dichrostachys cinerea.*

5.2 *Combretum apiculatum – Terminalia prunioides* sub-community

This sub-community is characterised by the high density of *Combretum apiculatum* and the presence of *Terminalia prunioides*.

5.2.1 *Acacia nigrescens – Ormocarpum trichocarpum* variant

This variant is found only in the Garonga section of the conservancy. Apart from the high diversity of *Combretum apiculatum*, it also contains a relatively high density of *Acacia nigrescens* and *Grewia* species as well as *Acacia exuvialis* and *Dichrostachys cinerea*.

5.2.2 Acacia exuvialis – Sclerocarya birrea variant

This variant is found mainly in the northern section of Garonga, but also occurs in the eastern section of Makalali between Mawelawela and Godiva roads. *Combretum apiculatum* is found in high densities as well as *Grewia* species. Other important species include *Dalbergia melanoxylon*, *Acacia nigrescens* and *Cissus cornifolia*.

5.3 *Acacia exuvialis – Strychnos madagascariensis – Dalbergia melanoxylon* sub-community

5.3.1 *Acacia nigrescens – Acacia exuvialis* variant

Although this variant is dominated by *Acacia nigrescens* and *Combretum apiculatum*, it is distinguished from other variants by *Acacia nigrescens* and *Acacia exuvialis*. *Dichrostachys cinerea*, *Ziziphus mucronata*, *Combretum hereroense*, *Flueggea virosa* and *Strychnos madagascariensis* are also prevalent in this variant, while the soils in this variant contain a high clay content (20.3%).

5.3.2 *Strychnos madagascariensis – Combretum apiculatum* variant

This variant is found in the higher part of the Conservancy, in the south western corner of the Makalali section and appears to be restricted to the coarse white sand found in this area. This variant appears to be associated with low percentage clay (Figure 2.10), low total cations (Figure 2.5) and zinc levels (Figure 2.8) and is also restricted to an

altitude of between 500 and 540m, above sea level (Figure 2.14). The characterising species in this variant are *Strychnos madagascariensis*, *Combretum apiculatum*, *Balanites maughamii* and *Combretum zeyheri*. *Strychnos madagascariensis* occurs in high densities here, while other species that occur in relatively high densities include *Acacia exuvialis*, *Commiphora glandulosa*, *Acacia nigrescens*, *Dichrostachys cinerea* and *Grewia* species.

6. Low closed grassland

All grasslands within the conservancy were assigned to this community. It could not be sub-divided based on the presence of different grass species, as only woody plants were sampled in the transects. Although this grassland community contained a few woody species, they occurred in very low densities and were predominantly shrubs below 1.5m in height. The woody plants found included *Grewia* species, *Acacia exuvialis*, *Combretum apiculatum*, *Commiphora africana*, *Acacia nigrescens* and *Ziziphus mucronata*. Most of the grasslands occurred in relatively small patches throughout the Conservancy.

7. *Combretum apiculatum – Dalbergia melanoxylon* low open woodland

Most of the aerial cover in this community is provided by grass, with a relatively low density of woody plants, most of which are shrubs under 1.5m in height. The species prevalent in this community include *Acacia exuvialis*, *Grewia* species, *Commiphora africana*, *Gymnosporia buxifolia* and *Dalbergia melanoxylon*. This community includes those areas in Garonga that have been bush-cleared.

8. *Combretum apiculatum – Grewia* low thicket

This community is found in patches in Garonga and near the western fence of Makalali and contains a high density of *Combretum apiculatum* and *Grewia* species. There are also, however, a relatively high density of other woody species including *Commiphora africana*, *Acacia nigrescens*, *Gymnosporia buxifolia* and *Acacia karroo*. 54% of the woody species are under 1.5m.

9. *Combretum apiculatum* low closed woodland

This woodland community is characterised by an extremely high density of *Combretum apiculatum* plants, with *Acacia nigrescens* and *Grewia* species having a density approximately one third that of *Combretum apiculatum*. Other species that occur in this community in relatively high densities include *Combretum hereroense* and *Sclerocarya birrea*. This vegetation community occurs in the north eastern corner of the Makalali section and extends from the Makalali – Garonga cutline in the north to the Makhutswi River in the south.

Discussion

Although only 107 woody plant species have been identified in the Greater Makalali Conservancy, and there does not appear to be a large variation in vegetation throughout the Conservancy, distinct vegetation types can be distinguished. These vegetation communities are separated by differences in the vegetation structure and species composition and density. These differences result in spatial heterogeneity at the Conservancy-level. This spatial heterogeneity and its maintenance is important in that a greater heterogeneity results in a greater species diversity (Rosenzweig, 1996). As a result, management decisions need to take this heterogeneity into consideration.

Certain areas may be of interest to management in that they have a high density of invasive shrub species as a result of past uses and management practices. White (1999) states that the proportions of woody plants in different height classes are closely related to past human disturbance, either in the form of firewood collecting or cattle farming. In areas where there is low disturbance, there are more plants taller than 2m than less than 1m (White, 1999). Invader species such as *Dichrostachys cinerea* (van Rooyen, Grunow & Theron, 1989, van Rooyen & Theron, 1989) and some *Acacia* species (van Rooyen *et al.*, 1989) also indicate the presence of past disturbance, overgrazing and the lack of certain natural browsers (van Rooyen *et al.*, 1989). These species are abundant in the low thickets, such as the *Cissus cornifolia – Commiphora africana* low thicket and some of the low closed woodlands. Another genus that appears to be invasive in the Greater Makalali Conservancy is *Grewia*. Individuals of this genus are found throughout the Conservancy and in most instances in fairly high densities. The high densities of woody plants in certain parts of the Conservancy may also have been brought about by the lack of burning, as there have been no fires in the Conservancy since 1985.

There are also areas in the Conservancy that are important in that they contain tree species unique to that vegetation type or species that are rare in that vegetation type. This is particularly the case in the Riperian low closed woodland, which contains the greatest diversity of plants, many of which occur only there and are also rare. This includes some of the *Acacia* species (*A. caffra*, *A. robusta*, *A. schweinfurtheii*) and some *Ficus* species (*F. ingens*, *F. sycamorus*). This vegetation type is also an important source of food for many of the vertebrate herbivores during the winter months, as it is often the only green vegetation during these months. The diversity in this vegetation type needs to be maintained, especially as it is seasonally flooded. This flooding,

if there has been extensive use of this vegetation type during the winter months, could result in loss of the vegetation, resulting in destabilisation of the river banks.

Because of the structural and species differences between all the vegetation types, each vegetation type will be important for different organisms at various temporal and spatial scales (Menge & Olson, 1990; Dekker, van Rooyen & Bothma, 1996). Some organisms may be restricted to a particular variant of a vegetation type, while others may move through all vegetation types, selecting certain types during different periods of the year (Dekker, *et al.*, 1996). An example is that of the Riperian low closed woodland, which is extensively used by all herbivores during the dry winter months. A good understanding of the relationships between various vegetation types, ecological preferences and the distribution of organisms, will therefore, aid in making informed management decisions.

The density of woody plants in the Greater Makalali Conservancy ranged from 1800 per ha to 5867 per ha, with the highest density being recorded in the *Colophospermum mopane* woodland. White (1999) states that the usual density in southern African game reserves is less than this, but that the density in the Sabi Sands Game Reserve, however, ranges from 4100 to 4800 per ha. The density in the Nylsvlei Nature Reserve (broad-leaf savanna) is 5800 per ha (Scholes & Walker, 1993). In communal lands, where there is a large amount of disturbance, the density per hectare is usually higher than in undisturbed areas and ranges from about 2100 per ha to 2800 woody plants per ha in the Newington region of Mpumalanga. This further indicates that there has been some disturbance in the past, which may have resulted in these high densities of certain species in the Conservancy.

In the same way that there is spatial variation in the vegetation, there is also spatial variation in all of the other Conservancy-wide variables that were mapped. The spatial heterogeneity in the Greater Makalali Conservancy is important in diversity and distribution studies of different species. Some species may not occur in an area because the factors on which they are dependent are not present or are present at levels too low to support them. However, spatial heterogeneity will not only determine the presence or absence of species, but also their abundance within the habitat in which they occur. Variables such as vegetation (Dangerfield & Telford, 1989; Hopkin & Read, 1992; Mwabvu, 1997; Zapparoli, 1992a) and soil factors (Kime, 1992; Tarasevich, 1992) have been shown to influence the diversity of various invertebrate groups. As a result, a good knowledge of the distribution and variation of these environmental variables is important in diversity studies and in understanding the distribution of species.

The potential role of each of the environmental factors quantified in this chapter on invertebrate diversity is assessed in Chapter Five.

CHAPTER 3
A STRATEGY FOR SAMPLING MILLIPEDES, CENTIPEDES AND SCORPIONS IN A SAVANNA ENVIRONMENT

Introduction

At present there is considerable effort being made to document and describe invertebrate diversity (Brennan, Majer, & Reygaert, 1999). This has been brought about by the Convention on Biological Diversity and the resulting change of conservation's principle goals to include the maintenance of biodiversity (Williams & Gaston, 1994). In order to accomplish the aims of the Convention and to determine the biodiversity of different areas, rapid and effective sampling and estimation procedures are required (Colwell & Coddington, 1994). This is especially the case with invertebrate biodiversity assessment, which is rarely considered cost effective (Oliver & Beattie, 1996) and is time consuming as a result of the range of sizes, behaviours and micro-habitats (Slotow & Hamer, 2000) occupied by these groups. Many different methods have been used to sample invertebrates in various environments, but in most cases there is no standard method for sampling a particular group of invertebrates. As a result, sampling methods need to be standardised to facilitate comparison between various studies (Brennan *et al.*, 1999) and habitat types.

There are two types of sampling methods, active and passive sampling. Passive sampling techniques (pitfall traps and other trapping techniques) have often been preferred in the past as they are considered to be repeatable and capture species active outside searching periods (Slotow & Hamer, 2000) such as nocturnal and less common species. However, there are a few drawbacks to using these methods. They do not collect the less mobile species and also collect a large number of species and individuals (Slotow & Hamer, 2000) that may not form part of the group or groups being studied. Time is thus spent sorting the sampled material in order to obtain the species under study. Those that are not required are often discarded or not accessioned, with the result that potential diversity and distribution information is wasted (Slotow & Hamer, 2000). Although active searching methods are able to capture less mobile species, they are not considered to be as repeatable as passive methods, although Slotow & Hamer (2000) suggest that their studies on millipedes and spiders indicate otherwise.

One of the passive sampling techniques that has been used extensively to undertake biodiversity studies and ecological monitoring as well as to study the occurrence, abundance and activity of

surface foraging invertebrates of different kinds is that of pitfall traps (Southwood, 1991; Topping & Sunderland, 1992; Longino, 1994; Mesibov *et al.*, 1995; Brennan *et al.*, 1999). This method involves setting a trap, leaving it for a period of time and then collecting whatever has been trapped at a later stage. The appeal of using this method is that pitfall traps are inexpensive, fairly easy to set up and operate (Southwood 1991; Majer, 1997), many species can be trapped, large catches often result and they are able to be replicated over space and time (Topping & Sunderland, 1992; Mesibov *et al.*, 1995). They cannot, however, trap all organisms and are only effective in collecting animals moving and searching for food on the soil surface or in the upper layer (Madari *et al.*, 1996).

Although pitfall trapping may be the most commonly used passive sampling technique for invertebrates there are a number of active searching techniques that have been used for various organisms. Visual observation involves an observer collecting or counting all organisms encountered *in situ* in a fixed area or time period (Southwood, 1991). This can be done in a number of different ways. One of these is the line transect method. The principle of this method is that the organisms an observer encounters while moving through an area is directly related to their density in that area (Southwood, 1991). The efficiency of this method will, however, differ in different habitats (Southwood, 1991) and may also be dependent on the ability of the observer to detect the organisms.

Another active searching method is that of sampling plots for a set period of time or sampling plots of a certain area (Ausden, 1997). The density of organisms sampled within each plot can then be used to provide a density estimate for a larger area. There is, however, the question of what plot size to use or how many plots should be sampled within an area to give an accurate estimate of the species present and their density. Nested quadrats have been used by plant ecologists to define species-area curves for plant communities (Krebs, 1989). The principle of this method is that the number of species increases with quadrat size but then plateaus at a quadrat size that determines the minimal area of the community (Krebs, 1989). As a result, a species-area curve can be constructed and used to determine the optimal quadrat size for a particular community. By searching a certain area or a site for a given time period, the unit effort can be standardised and in that way can be replicated between sites.

Both passive and active sampling methods have their own appeal and drawbacks. As a result, many studies have indicated that both types should be used in conjunction with each other as the use of one method may limit the accuracy of sampling. A study on ants in Australia showed that

rare species were under-sampled in the pitfall traps, while active searching a small area sampled these rare species (Majer, 1997). A study of the relative efficiency of passive sampling (pitfall trapping) and active searching for millipedes indicated that active searching by an experienced collector will often provide a longer species list than pitfall trapping (Mesibov *et al.*, 1995). However, other studies, such as that conducted by Melborne, Gullan & Su (1997) on crickets and slugs, have shown that pitfall traps generally indicate the actual abundance of species.

All of the methods mentioned above have been used, in some form, to sample millipedes, centipedes and scorpions. However, there have not been many studies that have sampled these invertebrates in the savanna environment or that have determined which are the most effective sampling methods.

Most of the millipede sampling that has been undertaken in the past has focused on sampling in forest or closed canopy environments as opposed to the more open savanna environment. Pitfall traps have been used by a number of authors to determine the abundance and distribution of millipedes (Dangerfield & Telford, 1991; Kime, 1992; Klinger, 1992; Tarasevich, 1992; Mesibov *et al.*, 1995; Madari *et al.*, 1996) while others have reported capturing millipedes using pitfall traps which were aimed at sampling other organisms (e.g. Trueman & Cranston, 1997). Cryptozoan traps (Dangerfield & Telford, 1991; Madari *et al.*, 1996), the sorting of litter (Tarasevich, 1992) or soil samples (Klinger, 1992) and active or hand searching (Klinger, 1992; Tarasevich, 1992; Mesibov *et al.*, 1995) have also been used to sample millipedes.

Sampling for centipedes has taken place in a variety of habitats from natural forests (Zapparoli, 1992a) to urban environments, such as the city of Rome (Zapparoli, 1992b). Two main methods have been used in sampling. These are the use of pitfall traps, (Klinger, 1992; Wytwer, 1992; Zapparoli, 1992a; Trueman & Cranston, 1997) and active searching under surface debris (Klinger, 1992; Wytwer, 1992; Zapparoli, 1992b). Other searching methods such as the searching of soil samples (Klinger, 1992; Wytwer, 1992) and the sieving of leaf litter (Wytwer, 1992) have also been used to sample centipedes in the past.

Scorpions have been sampled in a range of habitats. These vary from the Mediterranean region in Israel (Warburg, 1997), the Kruger National Park within the savanna ecosystem in South Africa (Lawrence, 1964; Lawrence, 1967), Table Mountain, South Africa (Eastwood, 1978) to the desert environment (Lamoral, 1979; Bridges, le Roux & van Aardt, 1997). One of the most extensively used scorpion sampling methods is that of active searching (Lawrence, 1964;

Lawrence, 1967; Eastwood, 1978; Warburg, 1997). During the day, active searching involves turning over surface objects (rocks, logs and other debris) and looking under the loose bark of trees or other ground cover (Eastwood, 1978; Sissom *et al.*, 1990; Warburg, 1997). Active searching at night, however, involves the use of ultra-violet lights (Sissom *et al.*, 1990; Warburg, 1997). Many scorpion species fluoresce under ultra-violet light and are therefore relatively easy to detect at night (Polis, 1990b). Sissom *et al.* (1990) suggest that the best method is that of active searching at night using a portable UV light. However, this method is not quantitative, but is rather used just to determine what species are present. Pitfall traps have also been used to sample scorpions (Sissom *et al.*, 1990; Margules *et al.*, 1994; Trueman & Cranston, 1997), although Sissom *et al.* (1990) suggest that the use of pitfall traps as well as active searching during the day yield less than one percent of the individuals observed by searching with ultra-violet light.

Although many methods have been used to sample millipedes, centipedes and scorpions, there is no consensus as to what sampling methods are best for which invertebrates in general or in the savanna environment in particular. Some studies have indicated that it may be best to employ a range of methods to adequately sample the diversity of a group or groups of organisms (Trueman & Cranston, 1997; Churchill & Arthur, 1999).

In this chapter, the effectiveness of six methods were tested to determine which method or combination of methods were the best for sampling millipedes, centipedes and scorpions in the savanna environment.

Methods

Sampling was carried out at Makalali Private Game Reserve (24°09'14"S, 30°41'56"E) in the Northern Province, South Africa during three sampling periods. These were February/March 1999, October/November 1999 and February/March 2000. The sampling in October/November 1999 occurred just after the first summer rains, while the both the other sampling periods were between the middle and end of the rainy season. During all sampling periods, sampling took place at various times after rainfall events. This ranged from a few hours to a few days after rain.

During each of the three sampling periods, three sites were selected in five habitat types in the reserve resulting in 45 sites being sampled throughout the reserve during the study. The five habitat types were determined visually, using differences in vegetation type and soil characteristics (Table 3.1). The habitat types sampled were three mixed bushveld types, all with different soil characteristics (brown loamy soil, coarse white sand and rocky ground cover), rocky outcrops and mopane woodland. The sand type classifications were based on the particle-size classes given in the Soil Survey Field Handbook (Hodgson, 1976). These habitat types were selected as they are relatively undisturbed by human activities such as burning and bush clearing.

Table 3.1. The factors used in determining each habitat type.

	White sandy bushveld	Brown sandy bushveld	General mixed bushveld	Rocky outcrop	Mopane woodland
Vegetation type	Mixed bushveld	Mixed bushveld	Mixed bushveld	Mixed bushveld	Mopane
Sand type	Coarse	Medium	Coarse	Coarse	Loamy
Soil colour	White	Brown	Brown	Brown	Brown
Rocks present	No	No	Yes	Yes	No
Boulders present	No	No	No	Yes	No

During the three sampling periods six different sampling methods were employed, although not all were tested in all sampling periods. During all sampling periods pitfall traps and active searching both nested and random quadrats were used. In February/March 1999 cryptozoan traps were tested, while the wet cloth and drive transect methods were tested for the first time during sampling in February/March 2000.

During the first sampling period in February/March 1999, all individuals that looked different (morphospecies) were collected. They were then all identified by taxonomists. The millipedes

were identified by Dr Michelle Hamer (University of Natal, Pietermaritzburg), the centipedes by Dr Marzio Zapparoli (Universita della Tuscia) and the scorpions by Lorenzo Prendini (University of Cape Town). From these identifications a description and key was drawn up so that all species could be identified in the field. All those individuals that I came across in the field that I had not seen before or was not sure of their identification were kept for later identification.

In order to quantify sampling effort and compare the efficiency of each sampling method, the total number of species sampled using each sampling method was divided by the total number of hours spent sampling using that particular method. This provided the number of species sampled per hour. The number of hours was calculated by adding the time spent setting up each method, sampling and identifying the individuals. In pitfall trapping, the time spent locating the pitfall traps and sorting in the laboratory was also included, however, the length of time that the pitfall traps were left out in the field was not included.

Pitfall traps

Ten pitfall traps were set at each site and left for a period of two weeks before being collected again. The pitfall traps used were glass test tubes with a diameter of 18mm and a height of 150mm. Larger pitfalls were not used as they would have required more labour to set up, which would have meant that less traps would be serviced in the same time period. Organisms other than the target organisms would also have been captured, which has ethical concerns especially in a conservation area. Different designs have been used for pitfall traps including rain covers. Although these prevent rain water from falling into the pitfall trap, they would have attracted attention to the pitfall trap from animals such as baboons or elephant with the result that some of the pitfall traps may have been removed or tampered with.

Each pitfall trap was a quarter filled with a solution consisting of three parts 70% ethanol alcohol and one part glycerol. This preservative solution prevents the invertebrates from eating each other and prevents decay (Ausden, 1996). Holes were made in the ground by knocking a metal stake into the ground, removing it and then placing the test tube in the ground such that the lip of the tube was flush with the ground surface and the edges were flush with the edge of the hole. The traps were set in two rows parallel to each other, but 10m away from the other. Each row contained five pitfalls, each of which was 10m from the next. The position of each test tube was marked by attaching a bright blue cardboard tag to a branch or clump of grass right

next to or above the pitfall trap. After two weeks the test tubes were removed and the contents of all the test tubes at each site placed into one honey jar and labelled. During each sampling period, the pitfall traps at all 15 sites were set up during a single day and then all were removed during a single day two weeks later. It took approximately 45 minutes to set up the pitfalls at each site. This varied between sites and sampling periods because of varying soil hardness, which was dependent on rainfall. It took approximately 20 minutes to locate and collect the pitfalls at a single site.

During the sampling period in December 1999, some of the pitfall traps were flooded during above average rainfall. This may have resulted in a reduced number of individuals being captured in the traps as some traps were filled with water, some of the organisms decomposed as a result of the diluted alcohol concentration in the traps and other invertebrates were washed out of the traps. Some traps were also not recovered during other sampling periods, as the marking tags or the traps themselves were removed by animals or the traps were buried by sand that had been washed over them.

The invertebrates caught in the traps were sorted in the laboratory. This involved separating the millipedes, centipedes and scorpions from the rest of the invertebrates. The species and number of individuals caught per site was recorded and in the case of the millipedes and scorpions, sex was also recorded. The sorting of all the sites from one sample period was completed in one day.

Active searching one 25m^2 square nested quadrat

Nested quadrats were used to determine the optimal size of the quadrats that should be used to sample millipedes, centipedes and scorpions. All active sampling took place between 7:30 and 17:00. One nested quadrat was sampled per site, with each nested quadrat consisting of five quadrats. These quadrats were 1m x 1m, 2m x 2m, 3m x 3m, 4m x 4m and 5m x 5m. A nested quadrat of five meter squared was chosen as it was considered to be a size beyond which it became impractical to sample using this method. The nested quadrat was randomly placed at each site. A 50m tape measure was laid out in a square 5m by 5m. The corners of the square were held in place by 22.5cm long pegs. The 50m tape measure also served as the outside boundary of the larger quadrat. Nylon ski-rope was cut to lengths of 8m, 6m, 4m and 2m. These ropes were used to mark the boundaries of the 4m x 4m, 3m x 3m, 2m x 2m and 1m x 1m quadrats respectively. The rope was also held in place by 22.5cm long pegs. This allowed the

edges of the sampling quadrats to easily be laid out around trees and through bushes, if necessary, while at the same time clearly marking the boundaries of the quadrats. Each full quadrat took approximately 10 minutes to set up.

Sampling within each quadrat involved turning over all litter material, rocks and branches that were in the quadrat and scraping up the top layer of soil using a small trowel, while searching for millipedes, centipedes and scorpions. All trees or plants that fell into the quadrat were also searched up to a height of approximately two meters for the three groups of invertebrates. Each plot was only searched once, although there were occasions where more than one person searched one plot. In these cases, each person would start at a different side of the quadrat and work towards the other until the whole quadrat had been sampled. Although the time taken to sample each plot was recorded, there was no time limit to sampling each quadrat. Each quadrat was searched, until the individual sampling was sure the whole quadrat had been satisfactorily sampled. The time taken to sample each plot ranged from 15 minutes to one hour, depending on the vegetation and grass density and the number of individuals sampling the plot.

All millipedes, centipedes and scorpions found in each quadrat were collected in honey jars and identified by me at the end of the sampling session. Once they had been identified, I recorded the sex and species of each individual captured and then released them. Any individuals that I was not sure of were kept for later identification by taxonomists.

Active searching ten 2.25m^2 random plots

Ten 2.25m^2 random quadrats were set up at each site. These sites were chosen in relation to their position from the nested quadrat and were set up and sampled after sampling in the nested quadrat had been completed. Three sites were set off each of two of the corners of the nested quadrat, while two sites were set off each of the other two corners (Figure 3.1). In order to determine how far from the corner the sites were to be, 10 random numbers were chosen by those sampling, before the quadrats were set up. These numbers referred to the number of steps that had to be taken from the corners of the nested quadrat before a random quadrat could be set up. The quadrats were always set up on the left-hand side of the sampler as he/she walked away from the nested quadrat. One sampler would walk the distance of the first random number along one of the imaginary lines and then set up the quadrat on their left-hand side. The next quadrat would be set up by using the following random number as the number of steps to walk from the previous quadrat. The first three numbers were applied to the first line sampled, the following

two numbers to the second line, the next two numbers to the third line and the final three numbers to the last sample line. Each 2.25m^2 quadrat was measured out and marked using five meter tape measures.

These quadrats were searched in the same way as the nested quadrats and all millipedes, centipedes and scorpions found were placed in honey jars. I recorded the number of individuals and their species for all three invertebrate groups, while I also recorded the sex of the millipedes collected. Once everything had been recorded, the specimens were released, while any individuals that I was not sure of were kept for later identification by taxonomists.

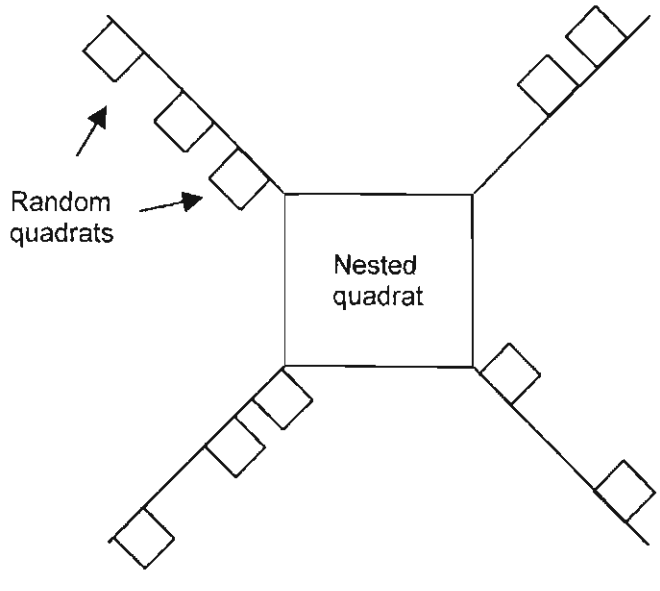


Figure 3.1. The positions of the ten random quadrats in relation to the nested quadrat.

Cryptozoan traps

At each site, two clear corrugated plastic sheets, measuring approximately 25cm by 25cm, were buried at random positions under approximately two centimeters of soil. A few small pieces of carrot and butternut were placed under the sheeting, as bait, and the traps were left in place for a period of two weeks. After two weeks, they were lifted and the numbers and species of all millipedes, centipedes and scorpions found underneath were recorded. If any millipedes were present, their sex was also recorded. All traps were laid on a single day and then also collected on a single day two weeks later. It took approximately 15 minutes to lay both traps at each site and 10 minutes to check and remove them after the two week period.

These cryptozoan traps were tested as it was thought they could be used as a refuge by the organisms under study. A period of two weeks was chosen in order to give enough time for the traps to be found and used as refuge sites by the invertebrates.

Wet cloths

This method is designed to attract millipedes to a damp refuge and samples species present in trees as opposed to ground-dwelling species. Harpagophorid millipedes are often found on trees in Makalali (pers. obs.) and could, therefore, be sampled using this method. Several millipedes and scorpions do live under bark or in crevices in trees where it is cool and presumably moist and as a result the wet cloths would be a way of sampling both invertebrate groups in this micro-habitat.

At each site two wet cloths were tied to two separate trees at a height of approximately 1.5m above the ground. The trees were randomly selected and included a wide range of tree species. The cloths were dark green cotton cloths (30cm long by 30cm wide), with the ends tied together. Each cloth was soaked in water before being tied up and was checked after a period of time to see if it had attracted any invertebrates. This period varied from two days to nine days. Each cloth was checked for invertebrates on at least two occasions and each time they were checked, they were re-soaked. Information noted for each site included the number of days since each cloth was checked and the weather conditions for the time period that the cloths were at each site.

Drive transects

This method was designed to sample millipedes, centipedes and scorpions as they crossed the roads in the various habitat types. Drive transects were conducted in the early morning (between 07:00 and 09:00) and late afternoon (between 16:30 and 18:30) for a period of 9 days from the 28th February to the 7th March 2000. Two routes (Figure 3.2) were selected based on the distance they covered in each of the five habitat types. During the 9 days this method was tested, each transect was driven in both directions four times, twice in the early morning and twice in the late afternoon. The driving speed was kept as constant as possible at 20km per hour. Each transect took between 40 and 75 minutes to complete and was carried out by two people. One drove the vehicle and looked predominantly on the right-hand side of the road for millipedes, centipedes and scorpions, while the other stood on the back of the vehicle and

looked predominantly on the left-hand side of the road. Data collected for each transect included an identification of each invertebrate found, its' GPS position, the start and end time for each transect, the distance of the transect and weather conditions, minimum and maximum temperatures and rainfall for the preceding 24 hour period. At the beginning of each transect the GPS (Garmin 12XL) was set to record the track taken at 10 second intervals.

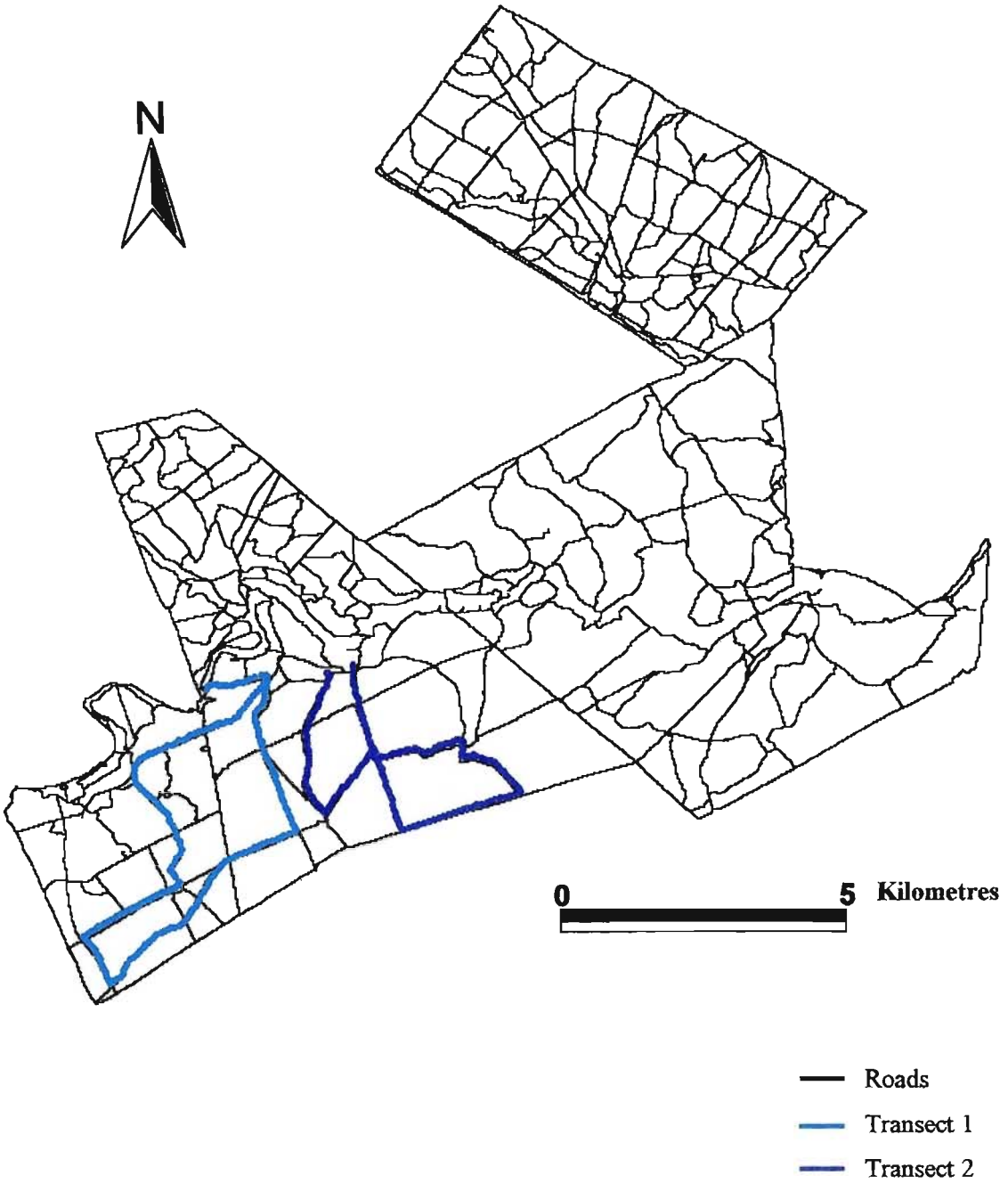


Figure 3.2. The position of the two invertebrate drive transects. The lines are superimposed dots, which were recorded every 10 seconds and allow estimation of variation in driving speed. The transects encompassed all of the habitat types sampled using the other methods.

Results

Appendix B provides a species checklist for all millipede, centipede and scorpion species sampled in the Greater Makalali Conservancy.

A list of all the sites and the pitfalls that were recovered at each site are given in Appendix C. All the pitfall traps from site 3.3 were listed as not being recovered, however although these pitfalls had been removed by baboons, some of the pitfalls that were found still contained scorpions. As only 13 out of 450 pitfall traps were not recovered for the scorpion sampling, it was not considered necessary to undertake any method of data standardisation between sites.

Millipedes

During the various sampling periods, 11 millipede species were sampled. Juveniles were sampled but were not included in the analysis as they could not be identified to species level.

The nested quadrat method sampled the greatest number of species (11) and individuals (665) (Figure 3.3). Both the pitfall traps and the random quadrats sampled the same number of species, although the random quadrats sampled a greater number of individuals. Both the cryptozoan traps and the wet rag methods were unsuccessful.

The large number of millipedes sampled in both the active searching methods was boosted by a large number of individuals (480) sampled at one of the rocky outcrop sites directly after a rainfall event using these active searching methods. However, the number of millipede individuals sampled in the pitfall traps at this site (6) fell within the range sampled at all the other sites. If the results from all sampling methods undertaken at this site are removed from the analysis, the number of species sampled using each method does not change. However, the total number of millipede individuals sampled in the pitfall traps decreases to 191, the number in the nested quadrats decreases to 344 and the number in the random quadrats decreases to 350.

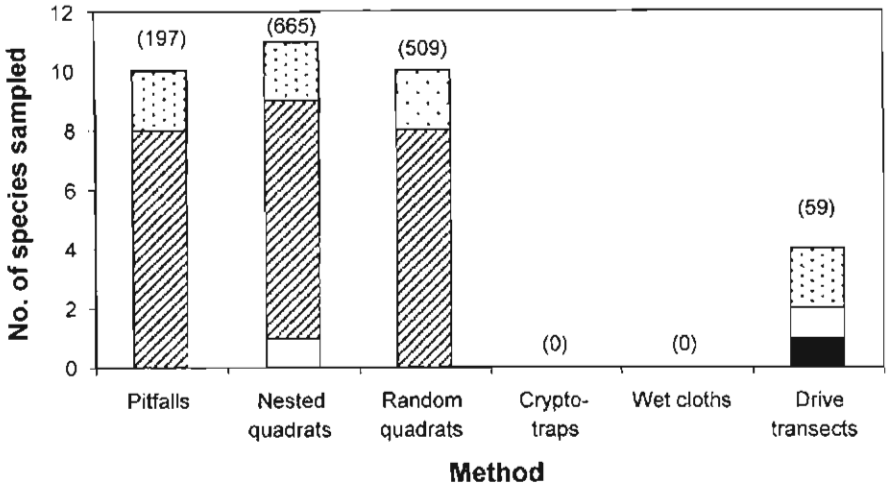


Figure 3.3. The number of millipede species unique to a method (black), shared with one other method (white), shared with two other methods (hatched) and shared with three other methods (dotted). The total number of species sampled by each method is indicated by the height of the bars, while the number of individuals sampled is given in parentheses.

Although the drive transect technique only sampled four millipede species, it was the only method to sample a species unique to that method. This was the large *Spinotarsus colosseus* species. The drive transects together with the nested quadrats were also the only two methods to sample the *Triaenostreptus* species. A possible reason for this is that both of these species are larger and able to range over a greater area than the smaller species. They may also occur at lower densities than the other smaller species with the result that they were not sampled in any other method. As a result, although the active searching methods may have provided a better estimate of the overall millipede diversity, the drive transect technique is an important method in sampling some of the larger millipede species. It is also the most efficient method, as far as time is concerned, as it sampled the greatest number of species per hour of sampling (Table 3.2). Both types of active searching methods are also important in sampling large numbers of the smaller species and many of the rarer species such as *Sphaerotherium modestum* (Table 3.3).

Table 3.2. The efficiency of each sampling method calculated as the number of species sampled per hour for each method.

	No. of species sampled per hour
Pitfalls	0.157
Nested quadrats	0.117
Random quadrats	0.090
Crypto-traps	0
Wet cloths	0
Drive transects	0.305

Table 3.3. The relative importance of the successful sampling techniques in sampling each species. R indicates species rarely sampled using that method, C commonly sampled, A abundantly sampled and a dash indicates that the particular method did not sample any individuals. Numbers in parentheses are the actual number of individuals sampled.

Family	Species	Pitfalls	Nested quadrat	Random quadrat	Drive transects
Spirostreptidae	*Lophostreptus ulopygus*	R (1)	R (2)	R (8)	-
Spirostreptidae	*Doratogonus rugifrons*	R (2)	R (2)	R (1)	C (27)
Spirostreptidae	*Doratogonus flavifilis*	R (3)	R (2)	R (4)	-
Spirostreptidae	*Triaenostreptus sp.* 1	-	R (5)	-	C (29)
Harpagophoridae	*Zinophora similis*	R (8)	C (43)	R (22)	R (2)
Odontopygidae	*Chaleponcus acanthophorus*	R (1)	R (9)	R (11)	-
Odontopygidae	*Spinotarsus colosseus*	-	-	-	R (1)
Odontopygidae	*Spinotarsus sp.* A	R (15)	A (207)	A (112)	-
Odontopygidae	*Spinotarsus sp.* B	C (75)	A (178)	A (188)	-
Dalodesmidae	*Gnomeskelus sp.*	C (59)	R (11)	R (5)	-
Sphaerotheriidae	*Sphaerotherium sp.* 1	R (8)	R (5)	R (7)	-
Sphaerotheriidae	*Sphaerotherium modestum*	C (25)	A (201)	A (151)	-

Note: R = less than 25 individuals sampled, C = 25 to 100 individuals sampled and A = greater than 100 individuals sampled.
Values not corrected for sampling effort and can therefore, only be compared within a particular method.

In order to determine what area would effectively sample a site, an accumulation curve was constructed for the nested quadrats (Figure 3.4). This was constructed by determining the mean number of species sampled in each area of the nested quadrat. Although the maximum number of species is sampled at $25m^2$, the means of both the $9m^2$ and $16m^2$ fell within the 95% confidence levels of the $25m^2$ area. This indicates that the $9m^2$ area may be the most effective area to sample.

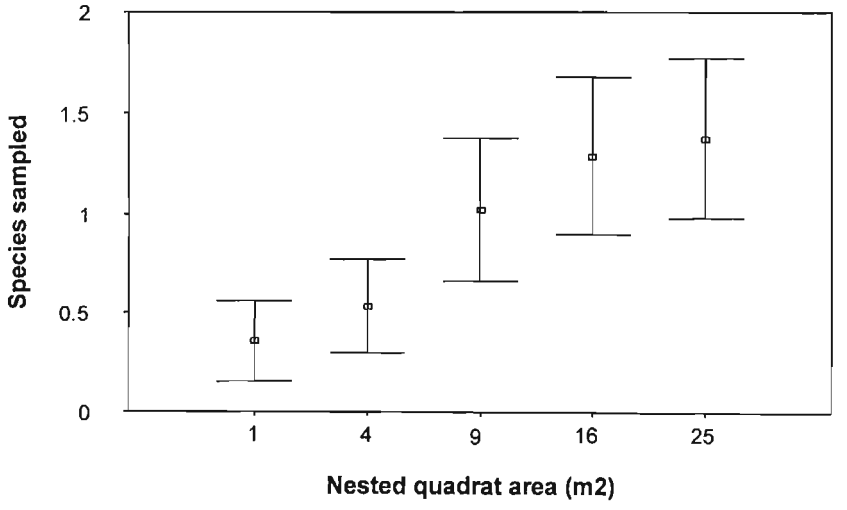


Figure 3.4. The accumulation curve for millipede species collected in the nested quadrats showing the increase in number of species sampled as area increases. The mean and 95% confidence limits are presented.

Centipedes

Three centipede species were sampled in Makalali during the study. Both the random quadrats and the nested quadrats sampled all three species, with the nested quadrat method sampling slightly more individuals than the random quadrats (Figure 3.5). The nested quadrat method was the most efficient method in that it sampled slightly more species per hour than the random quadrats (Table 3.4). It also sampled more *Scolopendra moristans* individuals than the random quadrats (Table 3.5). The crypto-traps and the drive transects did not sample any centipede species, while both the wet cloths and the pitfall traps managed to sample only one individual each.

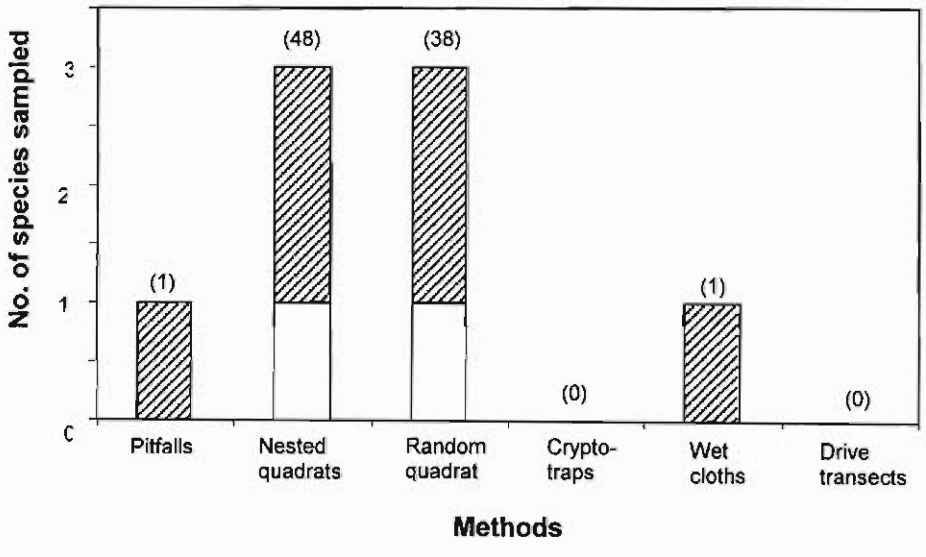


Figure 3.5. The number of centipede species shared with one other method (white) and shared with two other methods (hatched). The total number of species sampled by each method is indicated by the height of the bars, while the number of individuals sampled is given in parentheses.

Table 3.4. The efficiency of each sampling method calculated as the number of species sampled per hour for each method.

	No. of species sampled per hour
Pitfalls	0.016
Nested quadrats	0.032
Random quadrats	0.026
Crypto-traps	0
Wet cloths	0.024
Drive transects	0

Table 3.5. The relative importance of the successful sampling techniques in sampling each species. R indicates species rarely sampled using that method, C commonly sampled, A abundantly sampled and a dash indicates that the particular method did not sample any individuals. Numbers in parentheses are the actual number of individuals sampled.

Order	Species	Pitfalls	Nested quadrat	Random quadrat	Wet cloths
Geophilomorpha	*Orphaeus brevilabiatus*	-	R (5)	R (5)	-
Scolopendromorpha	*Scolopendra moristans*	-	A (33)	C (19)	R (1)
Scolopendromorpha	*Scolopendra* sp. 1	R (1)	C (10)	C (14)	-

Note: R = less than 8 individuals sampled, C = 8 to 24 individuals sampled and A = greater than 24 individuals sampled.
Values not corrected for sampling effort and can therefore, only be compared within a particular method.

The accumulation curve for the centipede species (Figure 3.6) collected using the nested quadrat method indicates that sampling an area of $25m^2$ was not sufficient to sample all of the centipede species as it is still increasing sharply at the largest area sampled. Only three species were sampled using this method although another three species have been found during ongoing research in the Conservancy. This suggests that a larger area may need to be searched in order to sample a site more accurately.

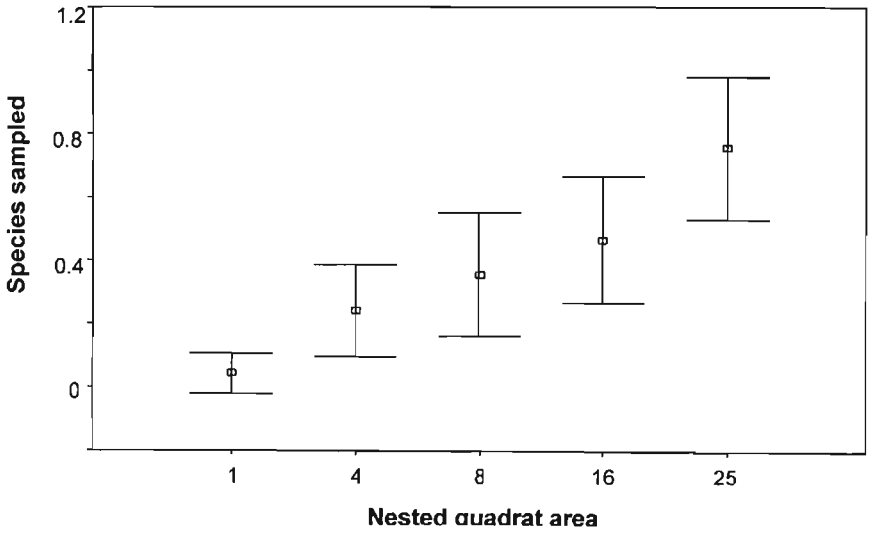


Figure 3.6. The accumulation curve for centipede species collected in the nested quadrats showing the increase in number of species sampled as area increases. The mean and 95% confidence limits are presented.

Scorpions

During the sampling in Makalali, eight scorpion species were sampled. All of these were sampled in the pitfall traps (Figure 3.7), while the random quadrats and nested quadrats were the only other methods to sample any scorpions. However, these methods only sampled 3 species and 7 individuals between them, while the pitfall traps sampled 69 individuals. The pitfall traps sampled five species that were unique to this method and another two species that were shared with the nested quadrat method. As a result, pitfall trapping was the most successful and efficient (Table 3.6) sampling method. Table 3.7 shows the species that were sampled by the active searching methods and the pitfall traps. No individuals were sampled using the crypto-trap, wet cloth or drive transect methods.

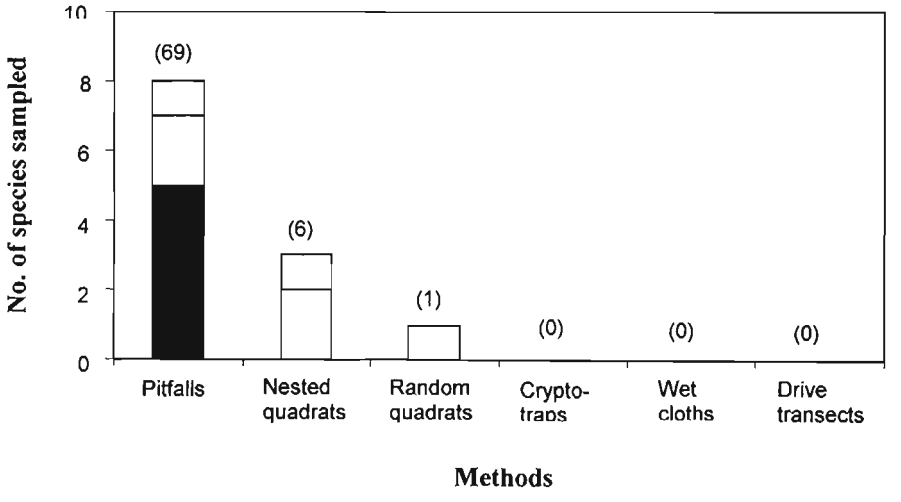


Figure 3.7. The number of scorpion species unique to a method (black), shared with one other method (white) and shared with two other methods (hatched). The total number of species sampled in each method is indicated by the height of the bars, while the number of individuals sampled is given in parenthesis.

Table 3.6. The efficiency of each sampling method calculated as the number of species sampled per hour for each method.

	No. of species sampled per hour
Pitfalls	0.125
Nested quadrats	0.032
Random quadrats	0.009
Crypto-traps	0
Wet cloths	0
Drive transects	0

Table 3.7. The relative importance of the successful sampling techniques in sampling each species. R indicates species rarely sampled using that method, C commonly sampled, A abundantly sampled and a dash indicates that the particular method did not sample any individuals. Numbers in parentheses are the actual number of individuals sampled.

Family	Species	Pitfalls	Nested quadrats	Random quadrats
Scorpionidae	*Cheloctonus jonesii*	R (1)	-	-
Scorpionidae	*Hadogenes troglodytes*	R (1)	-	-
Scorpionidae	*Opistophthalmus boehmei*	R (2)	-	-
Scorpionidae	*Opistophthalmus glabrifrons*	R (2)	-	-
Buthidae	*Parabuthus mossambicensis*	A (27)	-	-
Buthidae	*Parabuthus transvaalicus*	C (20)	R (2)	-
Buthidae	*Uroplectus carinatus*	R (5)	R (1)	-
Buthidae	*Uroplectus olivaceus*	C (11)	R (3)	R (1)

Note: R = less than 7 individuals sampled, C = 7 to 21 individuals sampled, A = greater than 21 individuals sampled.
Values not corrected for sampling effort and can therefore, only be compared within a particular method.

The accumulation curve for the nested quadrats (Figure 3.8) shows that no scorpions were collected in the $1m^2$ area. The mean number of scorpion species sampled in each of the nested quadrat areas from the $4m^2$ area to the $25m^2$ area fell within the 95% confidence level for each of the other areas. This indicates that each of these areas are as effective as the others in sampling scorpions. The most time efficient area to sample would, therefore, be the $4m^2$ area. However, only six individuals were sampled at all sites using the nested quadrat method, indicating that this method is not a very efficient one.

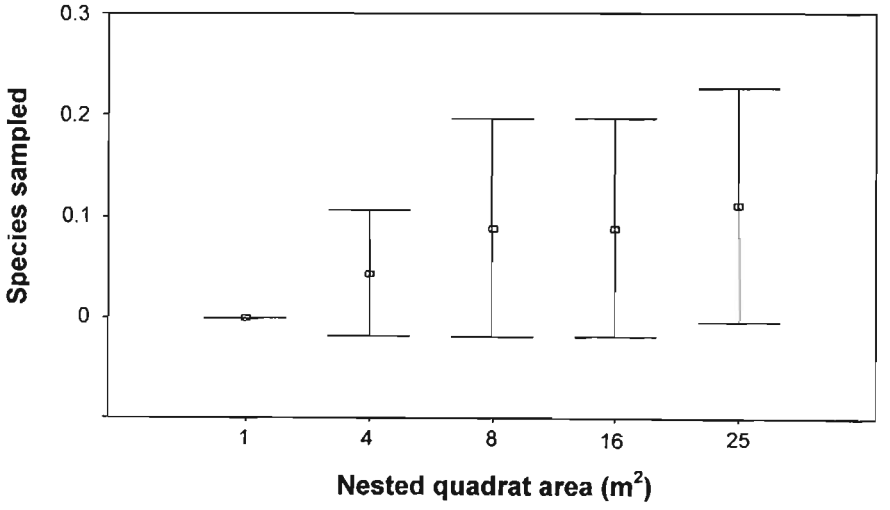


Figure 3.8. The accumulation curve for scorpion species collected in the nested quadrats showing the increase in number of species sampled as area increases. The mean and 95% confidence limits are presented.

Discussion

The results indicate that there are methods that sample each of the three invertebrate groups more effectively than others. Much of the success of certain methods can be related to the behaviour of the different groups and to the different species within those groups.

Millipedes in the savanna environment find shelter under stones, fallen stems, deserted termite mounds or other debris that may be lying around (Lawrence, 1984). The active searching methods employed in this study included searching under these potential shelters. As a result the active searching methods were the most successful, with the $9m^2$ nested quadrat (i.e. 3m x 3m from nested quadrat) proving to be the most effective way to sample most of the millipede species. The drive transect method is also an important method, especially for sampling the larger millipede species.

Millipedes also need moisture and cannot endure dry heat and unbroken rays of the sun (Lawrence, 1984). As a result, some species are nocturnal (e.g. *Sphaerotherium* species, Lawrence, 1984) while others move about in cloudy or wet conditions or during the cooler times of the day, such as early morning and late afternoon (Lawrence, 1984). Because of this they would have been active during periods outside of the sampling time and would be expected to be sampled using the pitfall traps. However, more of the smaller millipede species were captured using this method, while the larger species such as *Doratagonus rugifrons*, *Triaenostreptus sp.* 1 and *Zinophora similis* were sampled more successfully using the active searching methods (nested and random quadrats and drive transects). These larger species are able to range over a wider area and may also occur at lower densities than the smaller species. As a result, large numbers of these species would not be sampled using the pitfall traps. A further factor that may have reduced the success of the pitfall traps for the larger species, was the relatively small diameter of the pitfall traps. A study by Trueman & Cranston (1997) found that millipedes were sampled more effectively in large pitfalls as opposed to small. *Zinophora similis* has also often been seen on the branches and stems of trees in the Greater Makalali Conservancy (pers. obs.) and may, therefore, not spend much time on the ground. Because of this the pitfall traps would not be effective in sampling this species.

The results of the millipede sampling techniques in this study match those of Mesibov *et al.* (1995). They also found that active searching (hand-collecting in 10m diameter circular plots) provided a greater number of millipede individuals and a longer species list than that of pitfall trapping in their study sites in the forests of central Tasmania. As a result, they concluded that

hand-collecting by an experienced worker will often yield a longer species list than pitfall trapping (Mesibov *et al.*, 1995). In this study in the Greater Makalali Conservancy, only one more species was sampled using the nested quadrat as opposed to pitfall trapping, but 468 individuals more were sampled. There was also a difference of 156 individuals between the number of individuals sampled using the nested quadrat method and the random quadrat method. This suggests that that type of active searching undertaken (one large plot versus several smaller plots) may also be an important consideration in sampling method design.

The sampling methods tested for centipedes indicate that both types of active searching methods are the most effective techniques to employ. Both the nested quadrats and the random quadrats provided the same number of species, although the nested quadrats provided a greater number of individuals. However, the accumulation curve for the nested quadrats did not plateau within the $25m^2$ area sampled. This indicates that although this method may be the most effective in sampling centipedes, further sampling within a larger area will need to be undertaken to determine the minimal area that will need to be sampled using a single plot.

Centipedes are generally nocturnal (Lawrence, 1984) and find refuge under sheltered places such as stones or fallen logs (Lawrence, 1984). However, species belonging to the *Scolopendra* genus do venture out during the daylight hours, but prefer to do so on a cloudy or misty day or during the cooler hours of the day, around sunrise and sunset (Lawrence, 1984). Because of the sites they select for sheltering, one could expect to sample centipedes using an active searching method that involved looking under these shelters. This may have been the reason that almost all the centipedes sampled in the Greater Makalali Conservancy were found under rocks, stones, logs and leaf litter. Pitfall traps may also be expected to sample a large number of centipedes as they are mobile during the nocturnal hours when they go in search of food (Lawrence, 1984). Although other studies have found that pitfall traps are a good supplement to hand collecting (Klinger, 1992), this study indicates that it is not an efficient method to use in sampling in the savanna environment as only one centipede was caught using this method. However, a study by Trueman & Cranston (1997) found that centipedes were sampled more effectively in large pitfalls as opposed to small. As the diameters of the pitfalls used in this study were relatively small, this may have resulted in the low success of this method in the Conservancy.

Most scorpion species are nocturnal and would, therefore, have been active during periods outside of the sampling time. One would, therefore expect them to be sampled in the pitfall traps. This was the case, with all scorpion species and almost all scorpion individuals sampled

using the pitfall traps. Many of the pitfall traps even managed to capture more than one individual scorpion. Only three species (all buthids) were sampled by methods other than the pitfall traps. This indicates the effectiveness of the pitfall traps in sampling scorpions. Even though they are nocturnal, one would expect to sample scorpions wherever they find refuge. However, three of the species sampled in the Conservancy find refuge by burrowing. These species are *Cheloctonus jonesii* (Harington, 1978), *Opisthophthalmus boehmei* (Newlands, 1972; Lamoral, 1979) and *Opisthophthalmus glabrifrons* (Newlands, 1972; Lamoral, 1979). Although scorpion burrows were seen during the active searching or random and nested quadrats, they were not excavated and as a result, individuals that may have been there were not sampled. The other scorpionid species sampled only in pitfall traps, *Hadogenes troglodytes*, lives between cracks of rocks (Newlands, 1972; Lamoral, 1979) and as a result would also be difficult to sample using active sampling methods. However, in contrast to the scorpionid species, all the buthid species with the exception of *Parabuthus mossambicensis*, were sampled in the nested and random quadrats as well as the pitfall traps. The *Uroplectus* species all find refuge under stones, beneath the bark of trees and in the cracks and crevices of old tree stumps (Newlands, 1978). While some of the *Parabuthus* species construct burrows, others live under stones, logs and other debris (Newlands, 1978). Arboreal scorpions were not specifically searched for, although trees within each quadrat were searched up to a height of approximately 2m. Further sampling for these scorpions was not undertaken as this would have greatly increased the time taken to sample each site.

Although eight scorpion species were sampled in the Conservancy, there is at least one species in the Conservancy that was missed by all the sampling methods. That was an *Opisthacanthus asper* individual collected outside one of the buildings on the reserve.

One of the methods that has been suggested by many authors to be the best for sampling scorpions is that of using a spotlight or UV light to search an area at night (Sissom *et al.*, 1990; Warburg, 1997). Many scorpions luminesce at night and would, therefore, be easy to find while walking or driving through an area. This method was not tested in the Conservancy, however, due to the presence of large game (elephant and white rhino) and dangerous carnivores (lion, leopard and hyeana). As a result, although this method has been shown to be effective in certain areas, it cannot be used effectively in reserves where there are dangerous animals.

The numbers of millipede, centipede and scorpion individuals sampled using the pitfall traps may have been influenced by a number of other factors apart from population size (Southwood,

1991). The efficiency of the trap has been found to be influenced by the size and shape of the pitfall, the material of which it is made (Luff, 1975) as well as the vegetation cover (Sanderson, Rushton, Cherrill & Bryne, 1995). Small pitfalls have also been found to be more effective in catching small organisms and larger traps more effective in catching larger organisms (Luff, 1975). Although the effects of size, shape and material on the catch structure were not tested in this study, the greatest number of millipede individuals that were captured in the pitfall traps were the smaller species. However, pitfall size, did not seem to have an influence on the size of scorpions captured. Although the diameters of the pitfall traps were relatively small, they still sampled adults of the large scorpion species. These scorpions may have entered the pitfall traps for a number of reasons, possibly in search of prey or in an attempt to use the pitfall traps as refuges. One pitfall trap even managed to capture eight scorpions.

Although the most effective sampling methods were identified for each invertebrate group studied, there are possible reasons for the lack of results observed for some of the methods tested namely the wet cloth and the cryptozoan trap methods. The wet cloth method was tested during the summer rainfall period in December 1999. During this particular season, there was above average rainfall, which resulted in extremely wet conditions in some areas. During the period the wet cloths were set up for, the ground was moist and there would have been a large number of natural moist refuges for the invertebrates. This method was also only tested during a short period in the summer months, and would need to be tested further in the future. A better time to sample using this method may be towards the end of the summer months, when the amount of available moisture would be lower.

The cryptozoan traps were also only tested once, towards the end of summer during the February sampling period in 1999. These traps were only set out for a period of two weeks and baited with a small amount of butternut and carrot. This was set to target millipedes in particular. This method could be tested more extensively using other bait and could also be left out for a longer period. In order to make these traps more hospitable to millipedes, they could also be moistened with water and checked on a more regular basis. By leaving the traps out for a longer period, scorpion or centipede species may also be attracted as they could move into these traps in search of prey settling under these traps.

Although the most effective methods for each invertebrate group have been determined, they may not be the most efficient. In order for a particular technique to be an efficient one, it needs to sample the greatest number of species in the shortest time period. This is especially important

in rapid biodiversity inventories where the aim is to document the biodiversity of an area in a short period of time. Another factor that needs to be considered, is the difference in time periods of sampling between passive and active methods. Although a passive sampling method may be the most effective, it may require (as in the case of the pitfall traps in the Greater Makalali Conservancy) that the traps be set up and then left for a period of time before being collected. This may not be possible in all biodiversity surveys. As a result, the most efficient method will need to be contrasted with the most effective (if they differ) taking into consideration any time constraints on the sampling period. However, for some groups (e.g. scorpions) where passive methods may be the only method that adequately samples that group, active methods could be employed during the time period that the traps are out in order to supplement the passive sampling method.

One of the aims of the Convention on Biological Diversity is to maintain biodiversity (Williams & Gaston, 1994). In order to do this biodiversity needs to be documented, which requires the development of fast and efficient sampling methods so that large areas can be effectively sampled in a short period of time. This study has shown that there are particular methods for millipedes, centipedes and scorpions that can be used to efficiently sample these groups in a relatively short time period. This study indicates that future sampling in the savanna environment should use a combination of active searching quadrats of $16m^2$ and drive transects to sample millipedes, active searching $25m^2$ quadrats (or larger) for centipedes and pitfall traps in the case of scorpions. Methods for effectively sampling other invertebrate groups will also need to be determined in order to ensure that sampling can become rapid and effective for these groups as well.

CHAPTER 4
MILLIPEDE, CENTIPEDE AND SCORPION DIVERSITY IN THE GREATER MAKALALI CONSERVANCY: HABITAT PATTERNS

Introduction

Insight into the distribution patterns of species is fundamental to an understanding of the biogeography and ecology of that species (Judas & Hauser, 1998). The occurrence of most organisms is governed by the distribution and abundance of biotic and abiotic factors in the environment. However, both types of factors operate on a range of scales and their effect varies between scales (Menge & Olson, 1990). Factors such as latitude and environmental energy have been shown to have an effect on the distribution and diversity of species at the global level (Gaston, 2000), while the small scale variation in some abiotic factors in an area produce significant heterogeneity in the occurrence and abundance of certain fauna (Dangerfield & Telford, 1992). Species distribution patterns are, therefore, dependent on a complex interplay between different spatial and temporal scale processes, as has been shown in various studies (e.g. Melton, 1987; Menge & Olson, 1990; Scogings, Theron & Bothma, 1990; Munthali & Banda, 1992; Dekker, *et al.*, 1996; Rosenzweig, 1996).

Because of the varying distribution of abiotic and biotic factors within the environment, different organisms will exhibit a heterogeneous distribution within an ecosystem. Some species are restricted by only a few variables (a wide tolerance range) and are therefore widely distributed. These species are referred to as generalist species. Specialist species (i.e. species that require a narrow range of specific conditions) will tend to be more restricted in their distribution, while generalist species will tend to be more widely distributed within an ecosystem. Areas that are more heterogeneous would, therefore, be expected to support a larger number of specialist species as these heterogeneous areas would contain a greater habitat variety with a greater potential for the availability of suitable micro-habitats for these species. Generalist species would also be supported in these habitats. As a result heterogeneous habitats would be expected to contain higher species diversity than more homogeneous habitats (Utez, 1979; Rosenzweig, 1996). This has been demonstrated in a number of studies on invertebrates (Greenstone, 1984; Dangerfield & Telford, 1992; Siemann, 1998).

It may not, however, be sufficient to study the relationship between species distribution and habitat types in one area and extrapolate the findings to another area, as some species, such as certain scorpion species, may occur in a different habitat in another region when their preferred

habitat is not available (Lamoral, 1979). As a result, relationships have to be determined and described within a particular area.

Millipedes have traditionally been thought to live primarily in the wet and damp soil of forests (Lawrence, 1984) with the result that most sampling has been undertaken in these closed canopy environments. They are not, however, restricted to forests, but also occur in drier areas, such as savannas (Lawrence, 1984). Much of the work on scorpion distribution has focussed on the desert habitat (Polis, 1990b), while most of the work on centipedes has been undertaken in Europe. Although a number of studies have shown that millipede activity is restricted to certain times of the year (e.g. Dangerfield & Telford, 1989; Dangerfield & Telford, 1991; Hopkin & Read, 1992; Madari *et al.*, 1996), not many studies have determined or described temporal variation in centipede or scorpion activity. There is therefore a general lack of knowledge about spatial variations in diversity and temporal patterns in activity for millipedes, centipedes and scorpions within the savanna environment.

The aim of this chapter is to determine and describe spatial patterns in diversity of millipedes, centipedes and scorpions in five habitat types in the Greater Makalali Conservancy. Regional and local specialists and generalists will also be identified. Their distribution within homogeneous and heterogeneous habitats within the Conservancy will be used to explain differences in diversity.

Methods

Sampling for millipedes, centipedes and scorpions was carried out in five habitat types in the Greater Makalali Conservancy using six sampling methods as described in Chapter Three. However, in order to determine the diversity and richness of each habitat type only three of the sampling methods (active searching random and nested quadrats and pitfall trapping) were included as they were used in all three sampling sessions. Diversity for each site was calculated by combining the results of all three methods per site and using Hill's diversity index N1.

Invertebrate richness per site was calculated by determining the total number of species sampled in the three sampling methods at each site. The mean and 95% confidence levels were then determined for the nine sample sites within each habitat type.

Evenness indices were not calculated or compared between habitat types as the number of species and individuals sampled were relatively small. As a result, evenness indices would have ranged from extremely high values to extremely low values, making comparisons between habitats very difficult.

Although the wet cloths, crypto-traps and drive transects were not included in determining the diversity and richness indices, the drive transect data were used in a separate analysis to determine the density of millipedes per habitat type sampled using this technique. This was done by dividing the number of millipede individuals sampled in each vegetation type by the total area sampled. Although visible road surface area varied between roads within the two transects due to different road widths and the presence of a grass strip in the middle of some roads, there was no difference in detectability of millipedes between the road surfaces of the different vegetation types. However, as each road was relatively uniform in its width, width measurements were taken at 10 points along each road to determine the average width for that particular road. These 10 points were equally spaced along each road and allowed me to determine the area within each habitat type that was being sampled. The roads in the Conservancy had been mapped by students from the University of Natal, Durban and Makalali Private Game Reserve staff using a Garmin 12XL GPS and the Cartalinx GIS program. I used this map in the ArcView GIS package to determine the distance of each road. Area sampled was then calculated by multiplying the distance sampled along each road by the average width of that road.

In order to determine if habitat or time of season (sampling period) had an effect on millipede, centipede or scorpion activity, a two-way ANOVA with interaction terms was run in the SPSS statistical computer program. Habitat, sampling period and the interaction of these two factors were used as the variables in the analysis. The residuals were tested for normality using the Kolmogorov-Smirnov test.

Tables were constructed for each invertebrate group showing the distribution of each species between habitats. This allowed me to determine, using the data from the sampling methods, which species were generalists and which were specialists at the local scale (the Greater Makalali Conservancy). A species was regarded as a local specialist if it was sampled in less than three habitat types, while those species sampled in three or more habitat types were regarded as generalists. Literature was used to determine whether species were specialists or generalists at the regional scale (southern Africa). Regional specialists were those species that had only been recorded in a particular part of southern Africa (e.g. Kruger National Park and Northern Province) while a species was regarded as a regional generalist if it had been recorded at a range of sites throughout southern Africa (e.g. Kruger National Park and Namibia).

As a larger number of millipede species were recorded in the Conservancy than centipedes or scorpions, I wanted to determine if millipede richness or diversity could be used as an indicator of centipede or scorpion richness or diversity. Millipede, centipede and scorpion diversity and richness were tested for normality using the Kolmogorov-Smirnov test. As the richness data were not normally distributed, a Spearman correlation was used to compare the richness of each invertebrate group. The diversity data, however, were normally distributed and as a result were compared using a Pearson correlation.

Results

Spatial variation

Throughout all the sampling undertaken, the millipedes were consistently the most species rich and most abundant taxon. The centipedes and scorpions were similar in both the number of species and the number of individuals sampled in each habitat type (Figure 4.1).

Millipede diversity was significantly influenced by habitat type (ANOVA: $F_{4, 45} = 6.419$, $P \leq 0.0001$). Although mopane woodland is a relatively homogeneous habitat type, dominated by one tree species, it is a very important habitat type for millipedes. The greatest number of millipede species (10) as well as the greatest number of millipede species unique to a habitat (1) and shared with one other habitat (2) were recorded in the mopane habitat (Figure 4.1). However, its mean diversity and richness was lower than both the rocky outcrops and the general mixed bushveld (Figure 4.2). The mopane woodland, together with the sandy mixed bushveld and rocky outcrop habitats were the only habitat types where millipede species were shared with only one other habitat type. Four millipede species were sampled in all the habitat types.

The rocky outcrop site contained the second highest number of millipede species as well as the highest number of individuals. However, 498 individuals (from seven species) collected at one site directly after a rainfall event would have resulted in the high number of individuals recorded in this habitat type. Although other sites were also sampled directly after rainfall events, these sites did not contain such large numbers of individuals. In order to determine how the results would change if such large numbers had not been sampled there, the site was removed from the analysis and the analysis re-run. However, the diversity values for the rocky outcrop habitat type did not change greatly, and the overall trend between the habitat types remained the same.

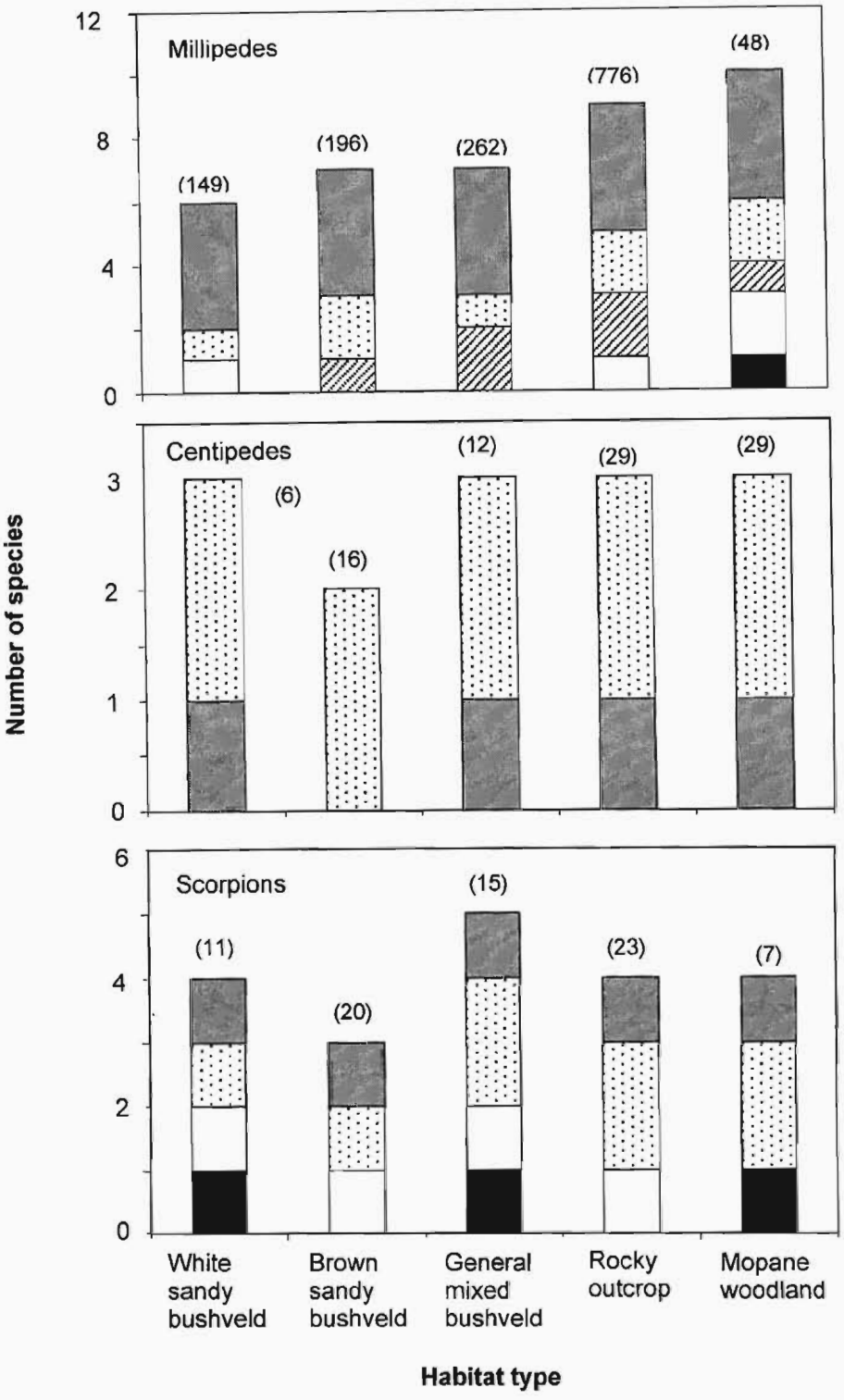


Figure 4.1. The number of species unique to a habitat (black), shared with one other habitat (white), with two other habitats (hatched), with three other habitats (dotted) and with four other habitats (grey). The total number of species sampled in each habitat type is given by the height of the bars, while the number of individuals sampled is given in brackets.

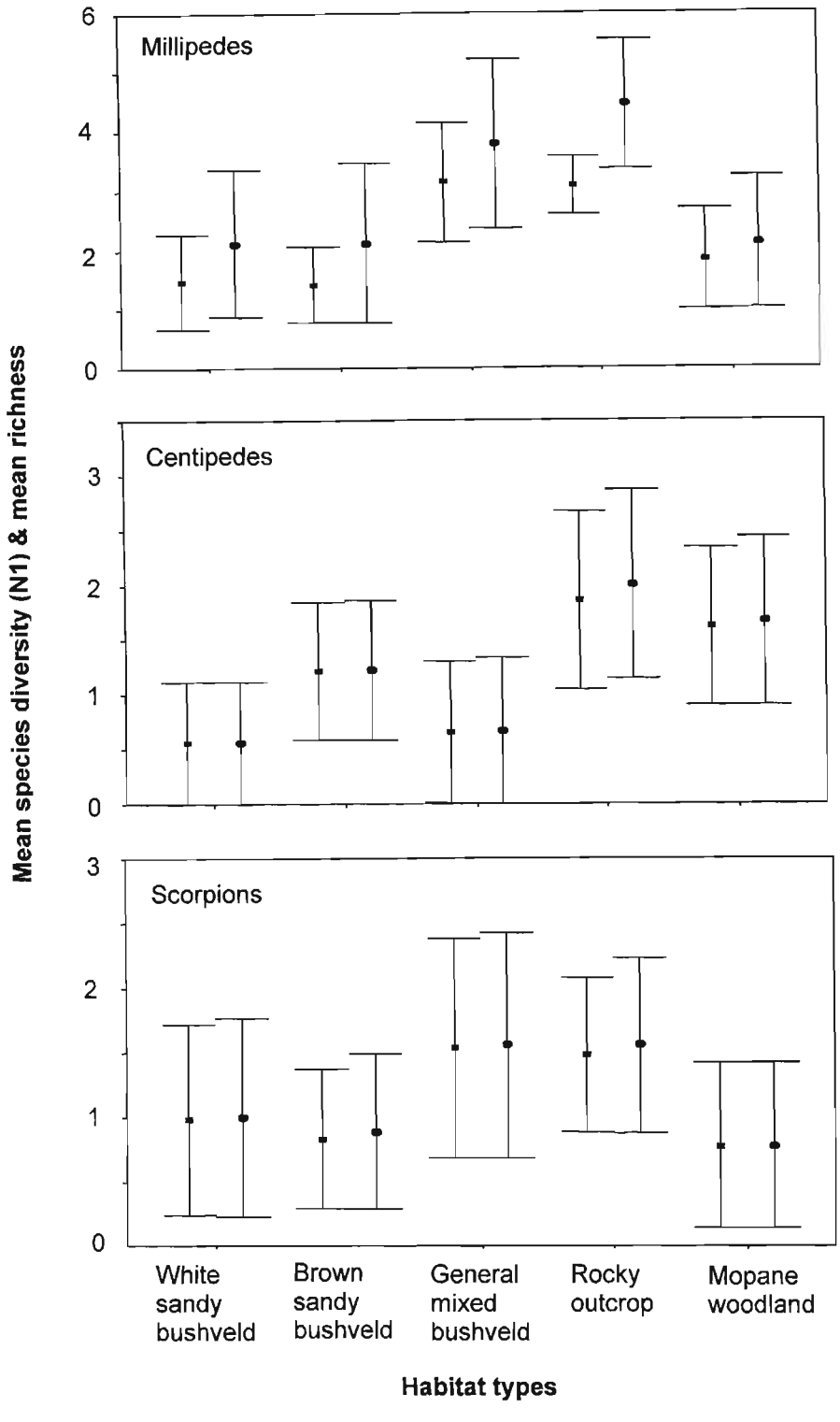


Figure 4.2. The range in mean diversity (Hill's diversity index N1), shown by squares, and mean richness (number of species), shown by circles, for each invertebrate group in each habitat type sampled in the Greater Makalali Conservancy. The 95% confidence limits are also presented.

Although the data from each sample site showed that the white sandy bushveld had both the lowest number of species and with the brown sandy bushveld, the lowest mean diversity index, the highest millipede density was sampled in this habitat type in the drive transects (Figure 4.3). The white sandy bushveld also contained a relatively high density of *Triaenostreptus* sp. 1 and *Doratogonus rugifrons* species, while the only *Spinotarsus colosseus* individual to be recorded during the study was collected in this habitat type as well. The only other individual of this species that has been observed in Makalali was found during September 1999 (Slotow pers. comm.[3]), indicating that this species may be very rare in the Conservancy. The active searching nested and random quadrats and the pitfall traps did not sample many *Triaenostreptus* sp. 1 or *Doratogonus rugifrons* species (Table 4.1), however these species were sampled in three habitats during the drive transects. These two species and the other species sampled using the drive transects (*Zinophora similis* and *Spinotarsus colosseus*) are species that are relatively large in size and would be expected to range over a much larger area than the smaller species. The success of the drive transect method in sampling these larger species emphasises the importance of this sampling method. These results also suggest that the white sandy bushveld may support a greater number of these larger millipede species than any of the other habitat types.

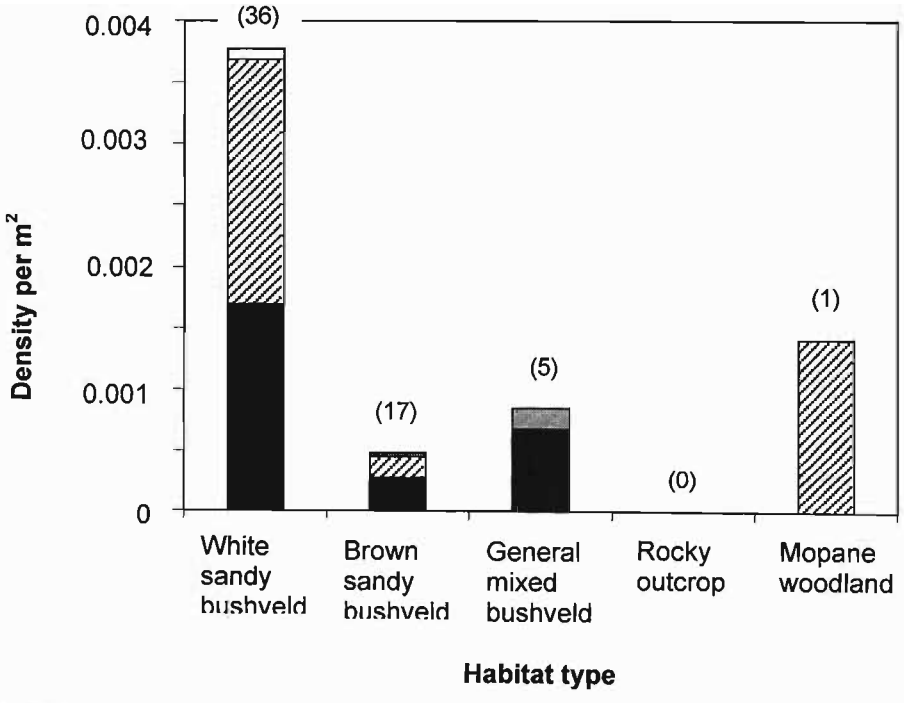


Figure 4.3. The density of each millipedes species sampled in each habitat type during the drive transects. Black indicates *Doratogonus rugifrons*, hatching indicates *Triaenostreptus* sp. 1, white indicates *Spinotarsus colosseus* and the grey colour indicates *Zinophora similis* species. The total density per vegetation type is given by the height of the bars, while the total number of individuals per vegetation type is in parenthesis.

[3] Dr. R. Slotow, School of Life & Environmental Sciences, University of Natal Durban , 4041, South Africa

Although *Lophostreptus ulopygus* appears to be limited to certain habitats and as a result was classified as a specialist (Table 4.1), this species has been observed in other habitat types in the Conservancy outside the sampling periods (pers. obs.). Most of the smaller species, with the exception of *Lophostreptus ulopygus*, were found in many of the sample sites within each habitat type. Although some of the larger species were also found in most of the habitat types, they were not found in many of the sample sites. They were recognised as generalists as they were sampled in a wide range of habitats in the drive transects.

Table 4.1. The distribution of millipede species between the habitat types as shown by the number of sample sites (maximum of nine) in which a species was found within each habitat type. D indicates those species sampled using the drive transect method. Their status, generalist (G) or specialist (S) is also given for the local (the Greater Makalali Conservancy) and regional scale (southern Africa). Figures in parentheses indicate the number of individuals sampled.

Species	White sandy bushveld	Brown sandy bushveld	General mixed bushveld	Rocky outcrop	Mopane woodland	Local	Regional
Lophostreptus ulopygus	0	0	0	3 (10)	1 (1)	S	S
Doratogonus rugifrons	3; D (3)	0; D	0; D	0	1 (2)	G	G
Doratogonus flavifilis	1 (2)	2 (5)	0	1 (1)	1 (1)	G	G
Triaenostreptus sp. 1	0; D	0; D	0	0	1; D (5)	G	S
Zinophora similis	1 (5)	3; D (13)	6; D (12)	6 (40)	3 (4)	G	G
Chaleponcus acanthophorus	0	0	0	1 (6)	0	S	S
Spinotarsus colosseus	0; D	0	0	0	0	S	S
Spinotarsus sp. A	6 (16)	3 (75)	8 (37)	9 (202)	3 (4)	G	S
Spinotarsus sp. B	5 (101)	4 (147)	6 (64)	5 (130)	3 (5)	G	S
Gnomeskelus sp.	3 (22)	3 (9)	6 (19)	3 (10)	4 (18)	G	S
Sphaerotherium sp. 1	0	1 (1)	3 (4)	4 (13)	0	G	S
Sphaerotherium modestum	0	3 (12)	5 (50)	8 (364)	2 (2)	G	S

Note: Generalist at the local scale = 3 or more habitat types, generalist at regional scale = widespread throughout southern Africa.
Specialist at the local scale = less than 3 habitat types, specialist at the regional scale = restricted to a particular part of southern Africa.

Only three centipede species were sampled in Makalali. Two of the species (*Orphaeus brevilabiatus* and *Scolopendra moristans*) were widespread and were sampled in all of the habitat types, while *Scolopendra* sp. 1 was sampled in all of the habitat types except the brown sandy bushveld. All three centipede species co-occurred in four of the habitat types, namely the brown sandy bushveld, general mixed bushveld, rocky outcrop and mopane woodland habitat types; both the rocky outcrop and mopane woodland types contained the highest number of individuals (Figure 4.1). However, the rocky outcrop habitat type (the more heterogeneous habitat) had a higher diversity index, due to a more even distribution of individuals between the species (Figure 4.2). The greatest number of individuals was also sampling in both these vegetation types. This indicates that a more homogenous habitat type, within the savanna environment at least, may not negatively influence abundance. The white sandy bushveld had

both the lowest mean diversity index and the lowest mean richness. Although only three centipede species were sampled there was a significant difference in mean centipede diversity between habitats (ANOVA: $F_{4,45} = 3.777$, $P = 0.011$).

As all three centipede species were widespread and recorded in almost all the habitat types, they were classified as generalists at the local scale (Table 4.2). Both *Orphaenus brevilabiatus* and *Scolopendra moristans* occur throughout the world and are generalists in the southern African region as well. Although *Orphaenus brevilabiatus* was described as a generalist, it was found in three or less sites within each of the habitat types, suggesting that it does not occur at high densities in these habitats. The unidentified *Scolopendra* species (*Scolopendra* sp.1) was described as a regional specialist, as it has not been described before and therefore no distribution records exist for this species.

Table 4.2. The distribution of centipede species between the habitat types as shown by the number of sample sites (maximum of nine) in which a species was found within each habitat type. Their status, generalist (G) or specialist (S), is also given for the local (the Greater Makalali Conservancy) and regional scale (southern Africa). Figures in parentheses indicate the number of individuals sampled.

Species	White sandy bushveld	Brown sandy bushveld	General mixed bushveld	Rocky outcrop	Mopane woodland	Local	Regional
Orphaenus brevilabiatus	1 (1)	0	2 (4)	3 (4)	2 (2)	G	G
Scolopendra morsitans	3 (4)	7 (10)	2 (3)	8 (19)	7 (18)	G	G
Scolopendra sp. 1	1 (1)	4 (6)	2 (5)	5 (6)	5 (9)	G	S

Note: Generalist at the local scale = 3 or more habitat types, generalist at regional scale = widespread throughout southern Africa
Specialist at the local scale = less than 3 habitat types, specialist at the regional scale = restricted to a particular part of southern Africa.

The highest number of scorpion species (5) was recorded in the general mixed bushveld habitat, while the lowest was recorded from the brown sandy bushveld type (Figure 4.1). The remaining habitat types all sampled the same number of scorpion species, with the greatest number of individuals being sampled in the rocky outcrop habitat type. The white sandy bushveld, general mixed bushveld and mopane woodland all sampled species unique to their habitat. However, these species were only sampled in a few sites within that habitat (Table 4.3) indicating that they are specialists and require certain environmental conditions that are fulfilled in those particular habitat types. All the habitat types, apart from the mopane woodland, had species shared with only one other habitat type indicating that each habitat type sampled is important in conserving scorpion diversity. *Parabuthus transvaalicus* was the only species recorded in all the habitat types. Two of the other buthid species (*Parabuthus mossambicensis* and *Uroplectes olivaceus*) occurred in three or more habitats and were recorded as generalists. However, all the

scorpionid species were restricted in their distribution between the habitats and were defined as local specialists.

Table 4.3. The distribution of scorpion species between the habitat types as shown by the number of sample sites (maximum of nine) in which a species was found within each habitat type. Their status, generalist (G) or specialist (S), is also given for the local (the Greater Makalali Conservancy) and regional scale (southern Africa). Figures in parentheses indicate the number of individuals sampled.

Species	White sandy bushveld	Brown sandy bushveld	General mixed bushveld	Rocky outcrop	Mopane woodland	Local	Regional
Cheloctonus jonesii	0	0	1 (1)	0	0	S	G
Hadogenes troglodytes	0	0	0	0	1 (1)	S	G
Opistophthalmus boehmei	2 (2)	0	0	0	0	S	S
Opistophthalmus glabrifrons	1 (1)	1 (1)	0	0	0	S	S
Parabuthus mossambicensis	0	5 (15)	5 (5)	2 (6)	1 (1)	G	S
Parabuthus transvaalicus	5 (7)	2 (4)	3 (3)	4 (5)	3 (3)	G	S
Uroplectus carinatus	0	0	4 (4)	2 (2)	0	S	S
Uroplectus olivaceus	1 (1)	0	2 (2)	6 (10)	2 (2)	G	S

Note: Generalist at the local scale = 3 or more habitat types, generalist at regional scale = widespread throughout southern Africa
Specialist at the local scale = less than 3 habitat types, specialist at the regional scale = restricted to a particular part of southern Africa.

Mean scorpion diversity was highest in the general mixed bushveld, although this was only slightly higher than that recorded in the rocky outcrops (Figure 4.2). The lowest mean diversity, mean richness and number of individuals were recorded in the mopane woodland. However, analysis showed that scorpion diversity was not significantly influenced by habitat type (ANOVA: $F_{4, 45} = 1.502$, $P = 0.22$).

Correlations run between mean millipede diversity and mean centipede and scorpion diversity indicate that it is possible to use millipede diversity as an indicator of scorpion diversity but not of centipede diversity (Table 4.4). However, correlation analysis between mean millipede richness and mean centipede and scorpion richness show that millipede richness can be used as an indicator of both centipede and scorpion richness (Table 4.5).

Table 4.4. The correlation of millipede diversity with centipede and scorpion diversity. All 45 sample sites were used in the correlation analysis.

	Centipede diversity		Scorpion diversity	
	r	P	r	P
Millipede diversity	0.234	0.123	0.296	0.048

Note: r = Pearson correlation coefficient

Table 4.5. The correlation of millipede richness with centipede and scorpion richness. All 45 sample sites were used in the correlation analysis.

	Centipede richness		Scorpion richness	
	r_s	P	r_s	P
Millipede richness	0.333	0.025	0.331	0.027

Note: r_s = Spearman correlation coefficient

Temporal variation

There was significant variation between sampling periods in the mean diversity index of millipedes (ANOVA: $F_{2, 45} = 0.001$) and scorpions (ANOVA: $F_{2, 45} = 0.005$), but not centipedes (ANOVA: $F_{2, 45} = 0.225$). The highest mean diversity index for the three groups was recorded early in the summer rainfall period during November 1999 (Figure 4.4). Although the combined effect of habitat and season was analysed, it did not significantly influence the diversity of any of the invertebrate groups. During the sampling period in March 2000, there was above average rainfall. Millipede and centipede diversity indices were higher in this period than during the same period in 1999, indicating that this high rainfall may have positively influenced their diversity. Scorpion diversity, however, was lowest during this period.

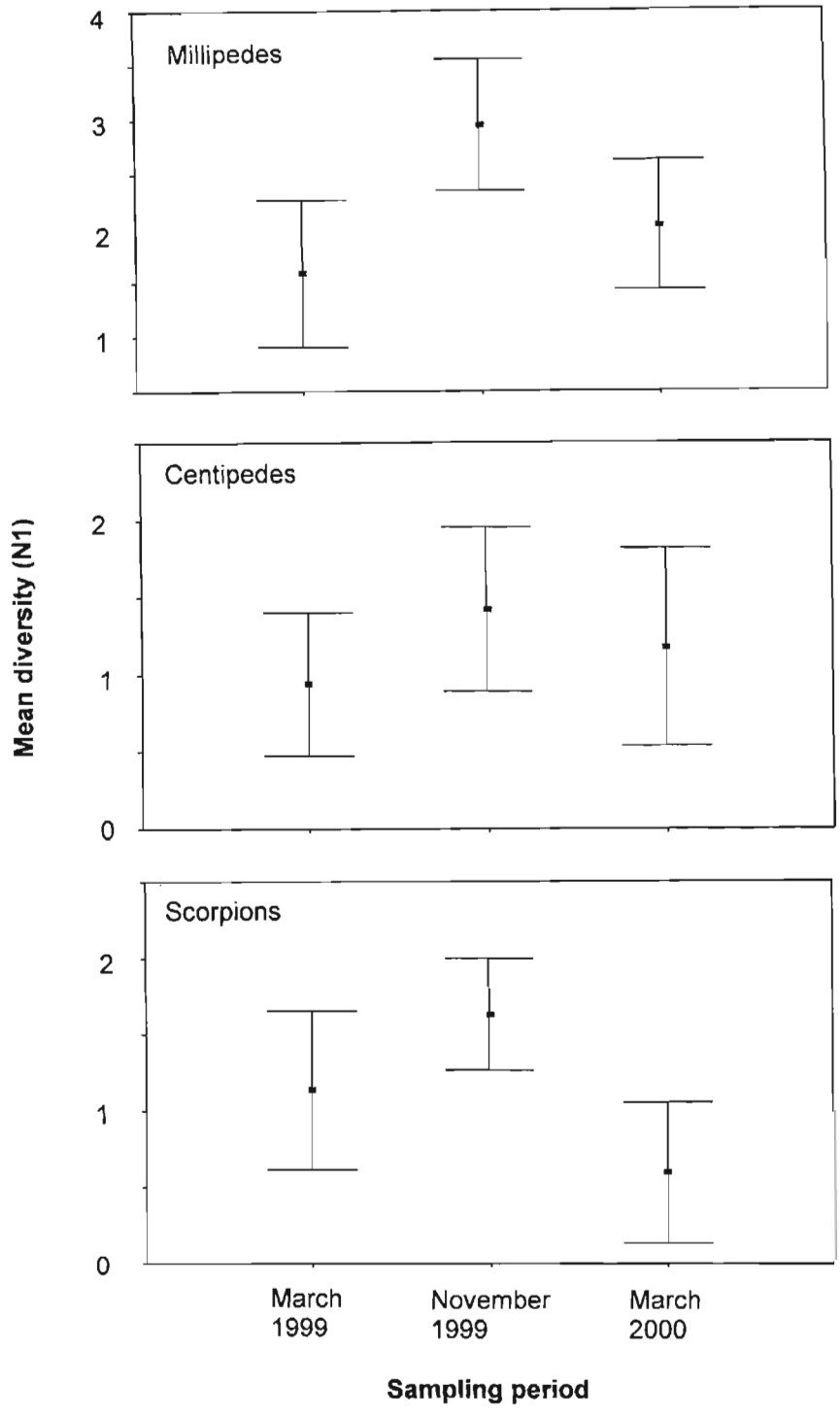


Figure 4.4. The variation in mean diversity for each sampling period showing the higher diversity for all three groups during the November 1999 sampling period. The 95% confidence levels are also shown.

Discussion

The results showed a significant difference in mean millipede and centipede diversity indices between habitats, with the more heterogeneous habitats supporting the greater mean diversity indices. The rocky outcrop and general mixed bushveld were the more diverse habitats, as although they contained a very similar vegetation type, they also contained rocks and boulders that would have provided a greater number of micro-habitats. The mopane woodland was considered to be the most homogeneous habitat type as it was dominated by one tree species, had minimal grass cover and no rock cover. Previous studies have also found higher millipede diversity in more heterogeneous habitats (Dangerfield & Telford, 1992; Mwabvu, 1997). Although there was no significant difference in scorpion diversity between habitat types, the highest mean scorpion diversity index was recorded in the two most heterogeneous habitats (rocky outcrops and general mixed bushveld) while the most homogeneous habitat type (mopane woodland) contained the lowest mean diversity. However, the highest centipede diversities were recorded in the rocky outcrop habitat followed by the mopane habitat. Although this may indicate that there may be no habitat effect on this group, habitat did influence centipede diversity. However, by taking into consideration the local specialist and generalist species within each of the three invertebrate groups, one can determine why, for both the millipede and scorpion species, the more heterogeneous habitats were more diverse than the homogeneous, but why this was not demonstrated with the centipedes.

Both the millipede and scorpion groups contained local specialist species while there were no local specialists within the centipede group. Diversity is higher in more heterogeneous habitats (Utez, 1979; Rosenzweig, 1996) as these habitats are able to support both specialists and generalists. This is because more heterogeneous habitats contain a greater number of micro-habitats which can support the specialist species. As there were no specialist centipede species, centipede diversity would not have been governed by differences in heterogeneity between different habitats. However, as both the millipede and scorpion groups contained specialist species, one would expect that more heterogeneous habitat types would support more specialist species, which in turn would result in greater species diversity within these heterogeneous environments and lower species diversity in more homogeneous habitats. This was demonstrated for both these groups in that a greater number of specialist species were found in these heterogeneous habitats, while the homogeneous habitats contained few or no specialist species.

Temporal variation for millipedes and scorpions was demonstrated, however, temporal scale had no effect on the diversity of centipedes. The highest diversity indices for all groups were recorded during the November sampling period. This was just after the beginning of the rainfall season. Other studies on millipede activity have also indicated that there is greater activity after the onset of the rainy season (Dangerfield & Telford, 1989) and that it decreases significantly about a month before the end of the rains (Dangerfield & Telford, 1991). The end of the rainfall season in the Conservancy is around March/April. The scorpion diversity appeared to be negatively affected by the above average rainfalls during the sampling in March 2000, while there was only a small difference in mean diversity for the millipede and scorpion species for the sampling during March 1999 and March 2000.

Millipede, centipede and scorpion species sampled in the Greater Makalali Conservancy were classified as specialists or generalists at the regional scale, based on literature. However, the factors influencing their distribution at this scale are different to those that operate at a smaller scale such as the local scale. Some species that were classified as generalists at the regional scale were restricted in their distribution between habitats at the local scale and were therefore specialists at this level. As a result, a species classification (as a generalist or specialist) at a regional scale would not necessarily influence its classification at the local scale. This was demonstrated in the millipede species, where many were classified as specialists in the regional scale, but at the local scale were classified as generalists. Some of the scorpion species, however, were regional generalists, but were found to be habitat specialists within the local scale. This emphasises the importance of studying the effects on diversity and distribution of different environmental factors at different scales. Factors that may restrict the distribution of species at a regional scale may have no effect on the distribution or diversity of these species at a local scale.

Present results indicate that even at the small scale that the study was undertaken, spatial and temporal effects on the distribution and mean diversity of millipedes, centipedes and scorpions can be observed. Often differences in diversity at the local scale are governed by the difference in heterogeneity between various habitat types. However, this is not always true, as was seen within the centipede group. However, it appears that, in general, this study concurs with others, with more heterogeneous habitats supporting higher diversity and higher numbers of specialist species.

Millipedes and scorpions are fairly widespread in their distribution throughout the Conservancy, although there are specialists within these two groups that are restricted to a limited number of habitat types. However, the centipedes are fairly widespread, with most of the species occurring in most of the habitat types. As a result, in order to conserve the highest diversity and richness for each group, different habitat types may need to be conserved for each of the species.
The difference in mean diversity between habitats and various invertebrate groups emphasises the importance of undertaking biodiversity studies of different invertebrate groups between various habitat types and highlights the importance of understanding habitat effects when planning conservation priority areas or habitat types for various invertebrate groups.

CHAPTER 5
MILLIPEDE, CENTIPEDE AND SCORPION DIVERSITY IN THE GREATER MAKALALI CONSERVANCY: MICRO-HABITAT INFLUENCES

Introduction

The distribution and abundance of both biotic and abiotic components in the environment govern the occurrence of most organisms. The relative importance of these factors varies with spatial (Menge & Olson, 1990; Gaston, 2000) and temporal scale (Dekker, van Rooyen & Bothma, 1996) and will vary between organisms (Beardall *et al.*, 1984). In order to understand patterns in the distribution of an organism, one needs to understand the processes underlying spatial heterogeneity. This involves determining, at a micro-habitat scale, those factors and processes affecting an organism's distribution and their relative importance to that particular organism. Once the factors underlying the spatial variation in community structure have been determined, this knowledge can then be placed into a predictive framework (Menge & Olson, 1990). This is important as it allows managers to determine areas that may be of conservation importance or areas that may contain a high diversity of a particular group of organisms.

The distribution of most organisms is governed by the distribution of factors such as the availability of food (Melton, 1987; Dekker *et al.*, 1996), water (Melton, 1987), shelter (Melton, 1987) and the distribution of predators (Melton, 1987; Dekker *et al.*, 1996; Warrick & Cypher, 1998). However, different species rate the importance of various factors within a habitat to a different extent (Melton, 1987). For many species, especially ungulates, a suitable habitat needs to provide water, minerals, shelter from climatic extremes (Melton, 1987), cover from predators and food (Dekker *et al.*, 1996; Melton, 1987). Studies in some vertebrate groups have found that the distribution of prey (Warrick & Cypher, 1998), predation risk (Warrick & Cypher, 1998), the abundance and quality of food (Merrill, Mattson, Wright & Quigley, 1999) and general resource availability (Mladenoff & Sickley, 1998) are important in the distribution of these vertebrate species within a habitat. Although a habitat may be suitable for a particular organism because it contains a factor that is important to that organism, the factor will in many cases be heterogeneously distributed within that habitat type. As a result, the organism will also be heterogeneously distributed within the habitat, concentrated in areas where there is a high abundance of the required factors or where the less desirable factors are less abundant.

Invertebrate groups would also be expected to respond to different habitat variables (Sanderson, Rushton, Cherrill & Byrne, 1995) based on food distribution, methods of acquiring food (whether they are predators or herbivores) and their shelter requirements. The distribution of millipedes, centipedes and scorpions is also influenced by different micro-habitat requirements. Although some studies have been undertaken to assess what habitat variables influence the distribution and diversity of these three invertebrate groups, most of this work has focussed on processes affecting their distribution in habitats other than the savanna environment. In the case of millipedes and centipedes the work has focussed on forested environments, whereas work on scorpions has focussed on the desert environments. Environmental variables such as vegetation (Dangerfield & Telford, 1989; Hopkin & Read, 1992; Mwabvu, 1997; Zapparoli, 1992a), litter (Bano, 1992; Kime, 1992; Tarasevich, 1992), soil factors (Kime, 1992; Tarasevich, 1992) and factors relating to the use of logs or branches and rocks as refuges (Lawrence, 1966; Lawrence, 1984; Polis, 1990b) have all been shown to have an influence on the distribution of these invertebrates within a habitat.

This chapter examines the processes affecting the spatial variation of millipedes, centipedes and scorpions at the micro-habitat scale. In order to achieve this, the micro-habitat factors responsible for the small scale distribution of organisms within a habitat were determined. GIS techniques were used to map these important micro-habitat characteristics over the Conservancy. The relationships between millipede, centipede and scorpion diversity and these micro-habitat variables were then used to produce a GIS-based model predicting their diversity in areas of the Greater Makalali Conservancy where no invertebrate sampling had been carried out.

Methods

Field sampling

In order to determine what environmental factors may influence the distribution and abundance of millipedes, centipedes and scorpions, detailed micro-habitat characteristics were collected at each of 45 invertebrate sampling sites. Information collected included rainfall, air and soil temperature, soil characteristics, vegetation cover, leaf litter cover, branch cover, rock cover, the presence of elephant dung and slope.

Although a number of different people assisted in field sampling during the period of the study, all micro-habitat data were recorded by myself. This ensured a standard estimate of each of the characteristics.

Rainfall

A rain gauge was set up at each of the 45 sites. During each of the sampling periods, the rain gauges were set up at only those sites that were being sampled during that period. As a result rainfall data were collected for different sites in late February to early March 1999, the end of October to mid November 1999 and mid February to late February 2000. All rain gauges were set up on the same day and all removed on one day two weeks later. These rain gauges recorded the total rainfall over the same two week period for each of the sites.

Air temperature

Minimum/maximum thermometers were set up at each of the 45 sites to record air temperature over a one week period. These thermometers were tied to the stem of a tree, at a height of approximately 1.5m above the ground. Each thermometer was set up on the southern side of the tree in a position where they would receive little or no direct sunlight during the course of the day. As with the rain gauges, thermometers were only set up at the 15 sites being sampled during that particular sampling period. These thermometers were set up from late February to the end of February 1999, the end of October to early November 1999 and mid February to late February 2000.

Soil temperature

The aim of measuring soil temperature was to determine the minimum and maximum temperature the surface soil at each site was exposed to over a one week period. Each thermometer was buried horizontally under a thin layer of soil in an area where the soil above the thermometer would receive maximum sunlight during the day. The amount of soil used to bury the thermometer was just enough to cover its surface (±1cm). The thermometers measured the minimum and maximum temperature of the soil covering them over a one week period. All thermometers were set up on the same day and removed a week later. The thermometers were set up at each of the 15 sites under study during the various sampling periods. As a result, the various thermometers were set up from the end of February to early March 1999, early to mid November 1999 and late February to the end of February 2000.

Vegetation cover

Various methods were used to estimate vegetation density at each of the 45 sites. Woody plant density was determined for the general area of each site, while grass and herb cover was determined for each random and nested quadrat sampled.

The density of woody plant species was determined using the PCQ (point-centred quarter) method. This method involves the use of two perpendicular straight lines which cross each other on the sample point (Bullock, 1996). They are used to create four quarters, within which trees are measured. To determine density, the woody plant nearest to the centre point in each quarter was sampled. Sampling involved noting the woody plant species as well as its distance from the centre point. In order to calculate density, the following equation (Bullock, 1996) was used:

$$\text{Density} = 1/(D_2)^2$$

where D_2 is the mean average of the distances of the four trees from the sample point (Bullock, 1996).

In order to separate out structural groups that may have an effect on diversity, two height classes were sampled. These were woody plants below 1m and above 2m. Plants below 1m may be expected to influence diversity as they may provide refuge, while those trees taller than 2m may influence diversity by providing shade. As a result, two sets of PCQ's were sampled at the same

point at each site. Some authors suggest that the direction of the PCQ should be set up in conjunction with compass points (Mueller-Dombois & Ellenberg, 1974; Bullock, 1996). However, during this sampling, the direction of the PCQ was randomly positioned for each PCQ measurement.

Grass and herb community cover was also recorded for each random and nested quadrat. This was recorded by estimating the percentage surface area of each quadrat covered by grass and herb species.

Shading

Shading was determined at each site by recording the percentage cover afforded by plants within each random and nested quadrat. This was recorded by estimating the percentage shade provided by the trees in and around each quadrat. The density of leaf cover on each tree as well as the position of the sun throughout the day in relation to trees surrounding the quadrats were used to estimate probable shade for each quadrat throughout the day.

Leaf litter cover

An estimate of the cover provided by leaf litter was recorded using two separate variables at each site. An estimate of the percentage of each nested and random quadrat covered by leaf litter as well as an estimate of the average leaf thickness within each quadrat were recorded.

Branch cover

Fallen branches have been found to serve as a shelter for millipedes in dry areas (Lawrence, 1966; Lawrence, 1984) and as a result may be an important refuge for other ground dwelling invertebrates in the savanna environment. In order to determine if fallen branches had an effect on the distribution of millipedes, centipedes or scorpions the percentage area within each nested and random quadrat covered by fallen branches was estimated. A list of the diameters of all branches found within each quadrat was also recorded and later averaged giving an average branch diameter for each quadrat. Branch diameter was recorded as the diameter at the middle of the branch.

Elephant dung

The dung of herbivores and other ruminants may also be an important micro-habitat factor for certain invertebrates as it often used as a suitable place for millipedes to lay their eggs and for the early larval stages after hatching (Lawrence, 1966). For this reason, the number of elephant dung balls in each quadrat was noted. Elephant dung may also provide a suitable refuge as fresh dung is moist and would provide a moist refuge away from heat. With time the dung dries out, which may reduce the appeal of the dung as refuge sites. As a result, the age of the dung was also estimated and recorded as being less or greater than six months old.

Rock cover

As rocks are known to provide suitable refuges for invertebrates such as millipedes (Lawrence, 1966; Lawrence, 1984), centipedes (Lawrence, 1984) and scorpions (Polis, 1990b), the percentage rock cover in each random and nested quadrat sampled was also recorded. The diameters (length at the widest part) of these rocks were also recorded and averaged to provide a measure of average rock size in each quadrat.

Slope

The slope at each quadrat was estimated by eye and recorded in degrees. Slope could be an important habitat variable on a small scale because it influences the speed of surface water run-off.

Soil

Soil samples were collected at each site and later taken for analysis by Cedara Agricultural College, Kwa-Zulu Natal. A large number of agriculturally important soil variables including soil sample density, phosphorus, potassium, calcium, magnesium, zinc, manganese, soil exchange acidity, total cations, percentage acid saturation, pH and near infra-red spectroscopy (NIRS) organic carbon and clay percentages were analysed. The soil was collected by digging to a depth of approximately 15cm using a hand trowel and then removing the soil that occurred from the surface to that depth and placing it in a soil sample box (60mm x 850mm x 90mm). Enough soil was collected at each site to fill one box. This involved collecting about four samples scattered among the quardats.

At each site, five soil samples were also taken for soil moisture content determination. These sets were randomly selected from five places at the sample site. This involved collecting five bags each with approximately 100g each of soil and measuring their weight (±0.1g) in the field using a small portable balance (KERN electronic balance, model 466-45). These soil samples were then oven dried at 105 °C for 24 hours. They were then re-weighed and the percentage soil moisture calculated from the difference in mass.

Micro-habitat data analysis

In order to ascertain which micro-habitat variables were important in determining the distribution and diversity of each of the invertebrate groups under study, a multiple regression analysis was carried out between all the variables listed above and the diversity of each of the three invertebrate groups. As a result, three separate regression analyses were carried out, one for all the millipedes, one for centipedes and one for scorpions. However, as invertebrate diversity, air temperature and soil temperature were calculated from sampling carried out during three separate sampling periods, the effect of sampling time had to be removed from the analysis. An ANOVA was carried out separately for each of the three invertebrate groups, air temperature and soil temperature with diversity, air temperature and soil temperature, respectively as the dependent variables and sampling period as the independant factor. The residuals from the analysis were used in the multiple regressions in place of actual invertebrate diversity, air temperature and soil temperature.

Other micro-habitat variables that were not collected in the field but were considered potentially important were also used in the analysis. These included vegetation type and aspect. Both these variables were determined for each site using the GIS based data given in Chapter Two. The sites were overlaid over the vegetation and aspect GIS maps and the values read off for each site.

Not all the variables collected in the field were used in the multiple regression analysis. Some were left out, as their effect on the diversity variable would have been covered by another variable used in the analysis (i.e. autocorrelated variables). A list of all those variables used in the multiple regression analysis is given in Table 5.1. The different aspect directions and the five vegetation types were each used as separate dummy variables. As a result, each site was recorded as either being present or absent in each vegetation type. The aspect of a sample site was recorded in a similar way. However, north and south were entered independently of the east

and west directions. Therefore, if a site was north-west, north or north-east facing it was recorded as being present in the north component, and if it was north-east, east or south-east facing, it was recorded as being present in the east component. As a result, a site could be recorded as being present in two directions.

Table 5.1. List of all variables included in the multiple regression analysis.

Vegetation density	Vegetation < 1m density
	Vegetation > 2m density
Grass & herb cover	Grass & herb cover (%)
Vegetation types	*Cissus cornifolia – Commiphora africana* low thicket
	Ziziphus mucronata – Combretum hereroense low closed woodland
	Combretum apiculatum – Terminalia prunoides low closed woodland
	Acacia exuvialis – Strychnos madagascariensis low closed woodland
	Colophospermum mopane low closed woodland
Leaf litter	Litter cover (%)
	Litter thickness (cm)
Branch cover	Branch cover (%)
	Branch size (cm)
Elephant dung	Number of dung balls
Soil	Total cations (cmol/L)
	Clay (%)
	Density (g/ml)
	PH
	Mn (mg/L)
	Moisture (ml/g)
	Zn (mg/L)
Temperature	Soil (°C)
	Air (°C)
Rainfall	Total rainfall (mm)
Rock cover	Rock cover (%)
	Rock size (cm)
Slope	Slope (°)
Aspect	North
	South
	East
	West

The multiple regression analysis was carried out using the STATISTICA statistical analysis computer program. A backward stepwise model was run and stopped at every step. This enabled me to stop the model at the highest R^2 value. Initially, all the variables and all the dummy variables were included in the model. However, before the model was run, I checked for redundancy and removed redundant variables. These variables were chosen based on their low tolerance values (Crawley, 1993). In all three regression analyses (millipedes, centipedes and scorpions), the number of elephant dung balls was redundant and the *Ziziphus mucronata – Combretum hereroense* low closed woodland vegetation type was non-significant. Both were, therefore excluded from further analysis. One of each of the vegetation and aspect dummy variables also had to be removed. These two variables were also selected based on their low

tolerance values. In the scorpion model, soil density and soil moisture were also redundant and excluded from the analysis. The model was then run and stopped at each step until the step that contained the highest R^2 value was achieved. All non-significant variables were then removed and the final model assessed using the beta coefficients to compare the effect of the various factors. Beta coefficients were used as they are standardised and allow the effect of each variable to be accurately compared (Zar, 1999).

Diversity model construction

Once the diversity of each of the three invertebrate groups and all the variables had been run through the multiple regression analysis, the significant results were used to produce a GIS-based model predicting diversity in areas in the reserve where sampling had not been carried out. Data for all the variables had been collected at each of the 45 sampling sites. However, these sites were not distributed evenly throughout the Conservancy, but were concentrated on the Rogers property, the western part of Makalali and in the north-eastern section of Garonga. Therefore, in order to increase confidence in the model, their values were extrapolated over the whole conservancy and then buffered for 1.25km around each sampling point (Appendix D). 1.25km was chosen as it allowed for the inclusion of areas between the sample sites where the highest density of sample sites were located. As a result, the model was only valid for a portion of the Conservancy.

Production of the coverages

Data relating to most of the factors used in the multiple regression analysis were only collected at the 45 invertebrate sampling sites. These included the vegetation density less than 1m and greater than 2m, grass and herb cover, litter cover, branch cover, rock cover and air and soil temperature. In order to produce a map of these variables for the Conservancy, values were interpolated from these sample points independently for each of the factors. The resultant maps were then buffered so that only those areas that fell within 1.25km of the sample points had values, while areas outside this buffer had no values.

All the soil variables that were needed for the model were used from the soil variable maps that were produced in Chapter Two. The rainfall map produced in Chapter Two was also used. Although some of the data for these variables was collected at sites other than just the 45

invertebrate sampling sites, they were still buffered for an area of 1.25km around each of the sample sites.

In order to produce coverages for each of the five vegetation types used in the analysis, the vegetation map (see Chapter Two) was resampled. Each vegetation type was given a value of zero, except for the vegetation type of importance, which was given a value of one.

The maps of north, south, east and west were produced from the aspect map (see Chapter Two). This map was reclassed to produce four maps, each showing one of the directions.

Production of the models

The multiple regression equation was used to relate all the significant factors (independent variables) to the dependant variable, in this case the residuals for the ANOVA between diversity and sampling period. In the multiple regression analysis in STATISTICA, both the beta coefficients and the partial regression coefficients are provided. The beta coefficients are standardised and are therefore comparable between coefficients. The partial regression coefficients, however, are non-standardised and represent the independent contributions of each independent variable to the prediction of the dependant variable (StatSoft Inc., 1999). As a result, the partial regression coefficients were used in the construction of the model.

The Map Calculator function in Arcview provides the means to relate different grid maps to each other. It allows one to undertake various calculations on different map layers and to multiply grid layers together. The equation explaining the diversity of each of the three invertebrate groups was used in the Map Calculator to relate all the significant map layers for each of the invertebrate groups together to produce a map showing the potential relative diversity for the buffered areas within the Conservancy. Maps for the significant factors that have not been presented in Chapter Two are contained in Appendix E through to Appendix H. Relative diversity was presented as opposed to actual diversity because the multiple regression equation explained the residuals from the ANOVA between diversity and sampling period rather than the actual diversity.

After the maps showing the predicted diversities of each of the focal groups had been created, maps of the actual diversity were also created. Although these two sets of maps were not

compared to determine how accurate the predicted diversities were, the presence of a map plotting the actual diversity aids in determining if there are any common patterns between them.

Use of the models

GIS models and other GIS information allow for the rapid analysis and testing of hypotheses of a large number of spatially distributed variables. Although detailed analysis of the accuracy of the models could have been undertaken, if was beyond the scope of the project to do so. However, the models were used to determine if there was any overlap in the predicted diversity of millipedes, centipedes or scorpions within the Greater Makalali Conservancy. As the maps showing predicted millipede, centipede and scorpion diversity were varied in their values, they needed to be standardised. In order to do this each of the maps was divided by the highest value present on the map, resulting in their values ranging from zero to one. The Map Calculator function in ArcView was used to carry out this procedure. The standardised predicted diversity models were then subtracted from each other, using the Map Calculator function in ArcView. Both negative and positive values are created, which relate to the higher diversity of one of the groups. The greater the value (either positive of negative), the greater the difference in diversity between the groups. Zero values on the resultant map indicate that the diversity of the two groups is exactly the same.

Results

Multiple Regression Analysis

Millipedes

Soil density was redundant in the millipede multiple regression and was excluded. When the model was run the first time, the north and east variables were non-significant and were, therefore, omitted in further analysis.

The final multiple regression analysis for the millipedes, produced a list of seven variables that significantly contributed to explaining the diversity (Table 5.2). Vegetation variables were the most important factors as vegetation density below 1m and the two vegetation types of *Combretum apiculatum – Terminalia prunoides* low closed woodland and *Cissis cornifolia – Commiphora africana* low thicket were significant contributors to diversity. Other vegetation related factors were the two variables of litter cover and the litter thickness. The most important variable contributing to millipede diversity was the vegetation density of woody plants under 1m, followed by leaf litter thickness and percentage leaf litter cover. Four of the variables (litter cover, litter thickness, vegetation less than 1m tall and the *Combretum apiculatum – Terminalia prunioides* low closed woodland) were positively correlated with diversity, while the other three (the *Cissus cornifolia – Commiphora africana* low thicket, south and west) negatively influenced diversity. Higher values within the first four variables, therefore, result in higher diversity, while areas that are predominantly south and/or west facing and the *Cissus cornifolia – Commiphora africana* low thicket result in a lower diversity.

Table 5.2. Factors affecting millipede diversity in savanna.

	Beta	B	$t_{(31)}$	p-level
Intercept		-1.55	-3.307	0.002
Vegetation < 1m density	0.439	1.095	2.774	0.009
Litter cover	0.332	0.404	2.753	0.010
Litter thickness	0.392	1.277	2.603	0.014
South	-0.315	-0.896	-2.485	0.019
West	-0.327	-0.856	-2.436	0.021
***Combretum apiculatum – Terminalia prunoides* low closed woodland**	0.279	0.893	2.391	0.023
***Cissis cornifolia – Commiphora africana* low thicket**	-0.260	-0.995	-2.157	0.039

Note: Beta = standardised β-coefficient
B = partial regression coefficient
Adjusted $R^2 = 0.530$, $F_{13, 31} = 4.82$, $p < 0.0002$

Centipedes

During initial analysis, the south and west variables were non-significant and excluded from the final regression.

The final regression model produced only four variables that significantly contributed to determining centipede diversity (Table 5.3). Three related to soil and ground structure. These were soil moisture, soil pH and rock size. Soil moisture was the most important variable, followed by soil pH. This indicates that the moisture of the ground plays an important role in determining the distribution of centipedes within a habitat. However, rainfall negatively influenced centipede diversity, indicating that although they require moist conditions, too much rainfall in an area will result in a low centipede diversity in that area.

Table 5.3. Factors affecting centipede diversity in savanna.

	Beta	B	$t_{(34)}$	p-level
Intercept		-0.564	-0.241	0.8110
Soil moisture	0.800	0.143	3.992	0.0003
Soil pH	0.458	0.630	2.990	0.0050
Rock size	-0.367	-0.0293	-2.536	0.0160
Rainfall	-0.528	-0.007	-2.435	0.0200

Note: Beta = standardised β-coefficient
B = partial regression coefficient
Adjusted $R^2 = 0.791$, $F_{10, 34} = 5.679$, $p < 0.0001$

Scorpions

Soil density was also redundant for the scorpion multiple regression model, while the south and east factors were non-significant in early analysis. These factors were removed from the final analysis.

The final multiple regression analysis for the scorpions produced only a few significant variables (Table 5.4). These factors were varied in their association, with the most important variables relating to soil conditions. Soil cations and soil pH were the most important variables, followed by air temperature and leaf litter thickness. Soil pH was, however, the only variable that positively influenced scorpion diversity.

Table 5.4. Factors affecting scorpion diversity in savanna.

	Beta	B	$t_{(34)}$	p-level
Intercept		-2.874	-2.095	0.044
Litter thickness	-0.365	-0.864	-2.415	0.021
Soil cations	-0.674	-0.103	-2.774	0.009
Soil pH	0.625	0.709	2.313	0.027
Vegetation < 1m	-0.325	-0.589	-2.058	0.047
Air temperature (residuals)	-0.320	-0.194	-2.370	0.024

Note: Beta = standardised β-coefficient
B = partial regression coefficient
Adjusted $R^2 = 0.29$, $F_{10,34} = 2.799$, $p < 0.0122$

Predictive GIS models of diversity

The GIS model was created using the significant variables identified in the multiple regression analysis. The multiple regression equations used in the production of each of the GIS models are given below:

The equation used to model millipede diversity was the following:

Y = -1.55 + (0.404)(litter cover) + (1.277)(litter thickness) + (1.095)(vegetation <1m density) + (0.893)(*Combretum apiculatum - Terminalia prunoides* low closed woodland) + (-0.995)(*Cissus cornifolia - Commiphora africana* low closed woodland) + (-0.896)(south) + (-0.856)(west)

The equation used to model centipede diversity was the following:

Y = -0.564 + (-0.0293)(rock size) + (0.143)(soil moisture) + (0.630)(soil pH) + (-0.007)(rainfall)

The equation used to model scorpion diversity was the following:

Y = -2.874 + (-0.365)(litter thickness) + (-0.674)(soil cations) + (0.625)(soil pH) + (-0.325)(vegetation <1m density) + (-0.320)(air temperature residuals).

The map showing the predicted relative diversity of millipedes (Figure 5.1) shows that there are distinct predicted 'hotspots' of diversity in the Conservancy. The predicted diversity hotspots in the centre of the Conservancy match the observed diversity, however, low diversity was recorded in the predicted hotspots in the south western section of the Conservancy. The predicted high diversity for the hotspots appears to be driven primarily by litter cover, which

also has a high density at these points. Although other variables, such as the *Combretum apiculatum – Terminalia prunioides* low closed woodland vegetation type, vegetation density less than 1m and litter thickness are also positively correlated with millipede diversity, they do not have as strong an effect on predicting diversity as does litter cover.

The predicted centipede diversity (Figure 5.2) shows distinct hot and cold spots throughout the Conservancy. The hotspots match the areas of high soil moisture, while the coldspots appear to match the areas with bigger rocks. Rainfall and soil pH did not seem to play much of a role in determining centipede diversity in this model. The predicted diversity in some parts of the Conservancy also matches the observed diversity fairly well.

However, the predicted scorpion diversity did not appear to match the observed diversity very well (Figure 5.3). The areas of highest predicted diversity are concentrated in the south western corner of the Conservancy, against the southern fence of Rodgers and at a few points along the Garonga southern and eastern fences. However these areas generally contained low scorpion diversity. The predicted diversity does not have many distinct hotspots, although there are a number of coldspots in the nothern parts of Makalali. The coldspots are associated with the soil variables in the model, and although soil pH has a positive effect on scorpion diversity, its effect is cancelled out by the strong negative effect that the total soil cations have on diversity. As a result the coldspots are associated with the areas where the total soil cations are high.

Differences in predicted diversity

The results from the analysis undertaken on the predicted diversities of the three focal groups, indicate that there are differences between their predicted diversities. Predicted centipede diversity was higher than predicted millipede diversity for most of the Conservancy (Figure 5.4), although there were a few spots where millipede diversity was predicted to be higher than that of the centipedes. However, predicted millipede and scorpion diversity was similar for most of the Conservancy (Figure 5.5), although there were predicted 'hotspots' for both invertebrate groups. Predicted centipede diversity was also greater than predicted scorpion diversity through much of the Conservancy (Figure 5.6), although scorpion diversity was predicted to be higher than centipede diversity in the south western corner of the Conservancy.

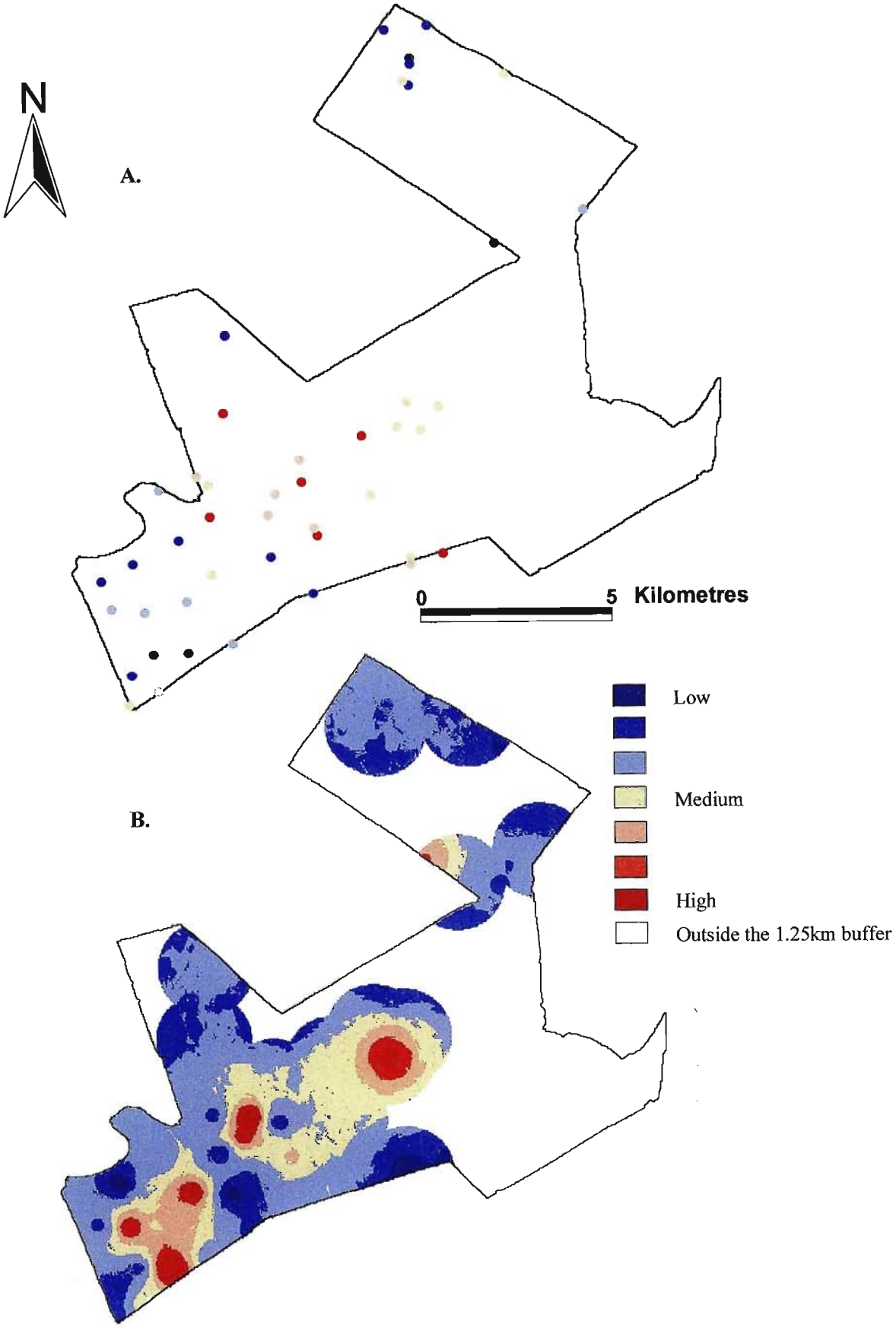


Figure 5.1. The relative measured (A) and predicted (B) millipede diversity for the Greater Makalali Conservancy. All areas further than 1.25km from sample sites were excluded from the predicted diversity map (white areas).

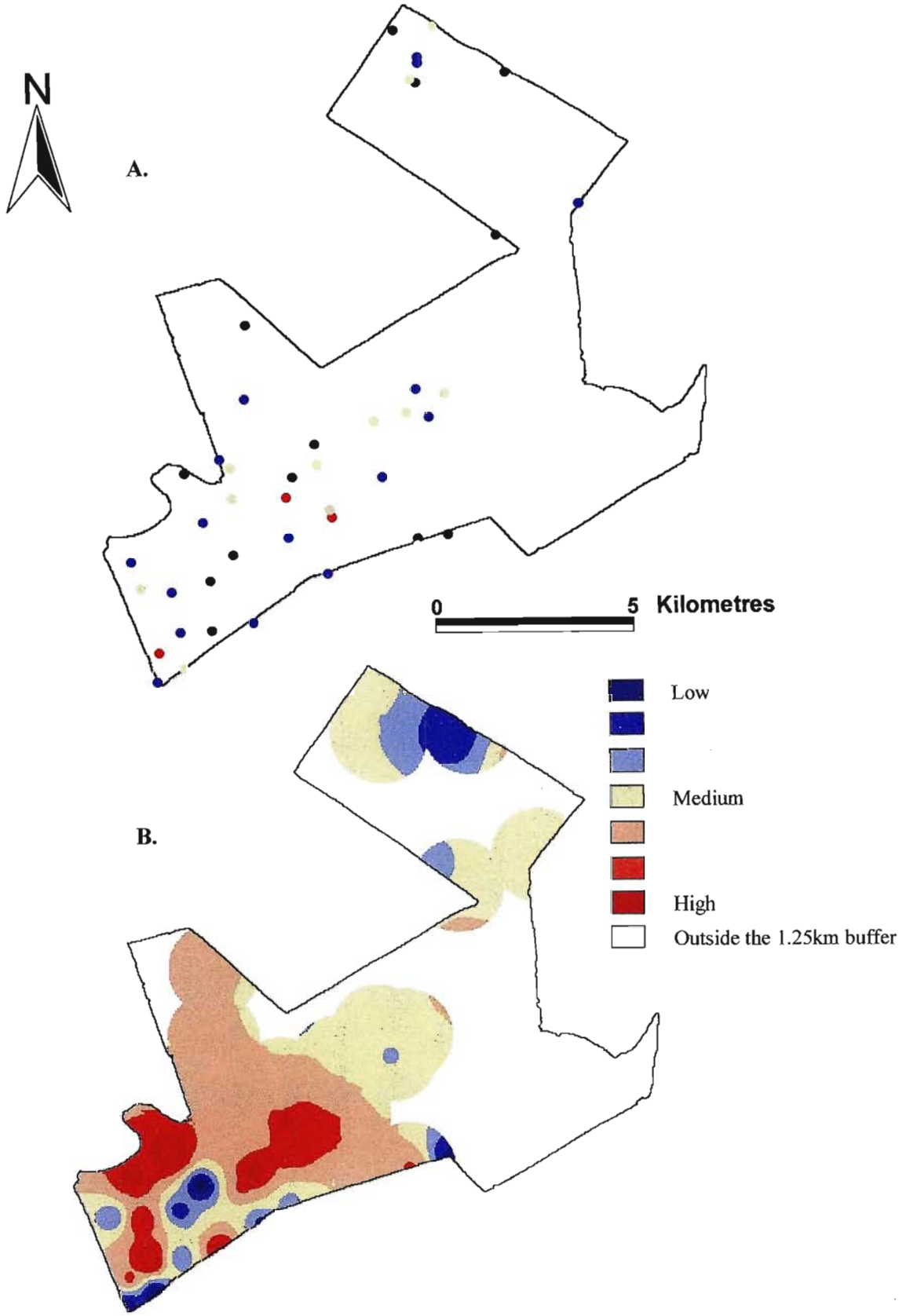


Figure 5.2. The relative measured (A) and predicted (B) centipede diversity for the Greater Makalali Conservancy. All areas further than 1.25km from sample sites were excluded from the predicted diversity map (white areas).

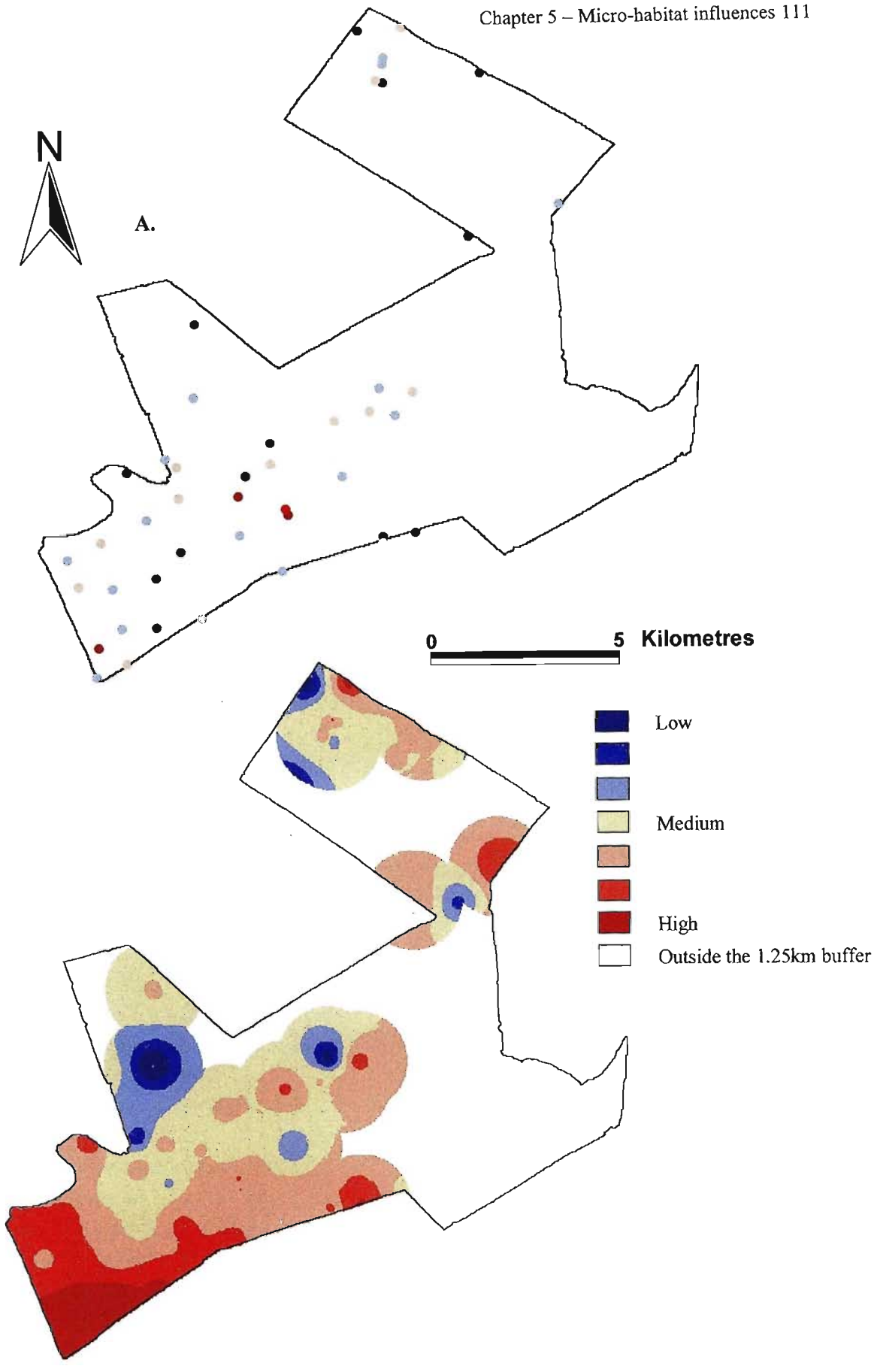


Figure 5.3. The relative measured (A) and predicted (B) scorpion diversity for the Greater Makalali Conservancy. All areas further than 1.25km from sampling sites were excluded from the predicted diversity map (white areas).

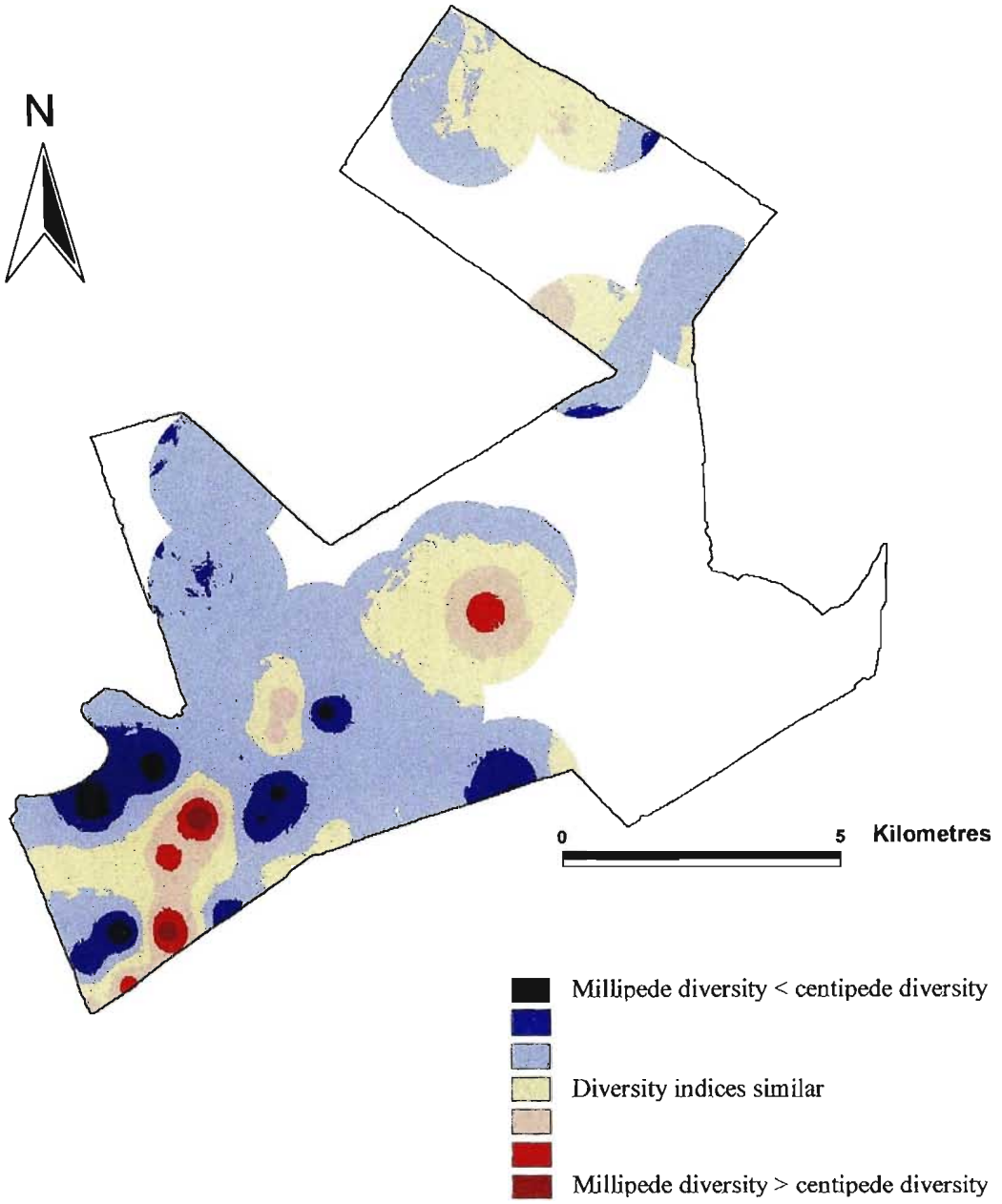


Figure 5.4. The difference in predicted diversity between millipede and centipede groups.

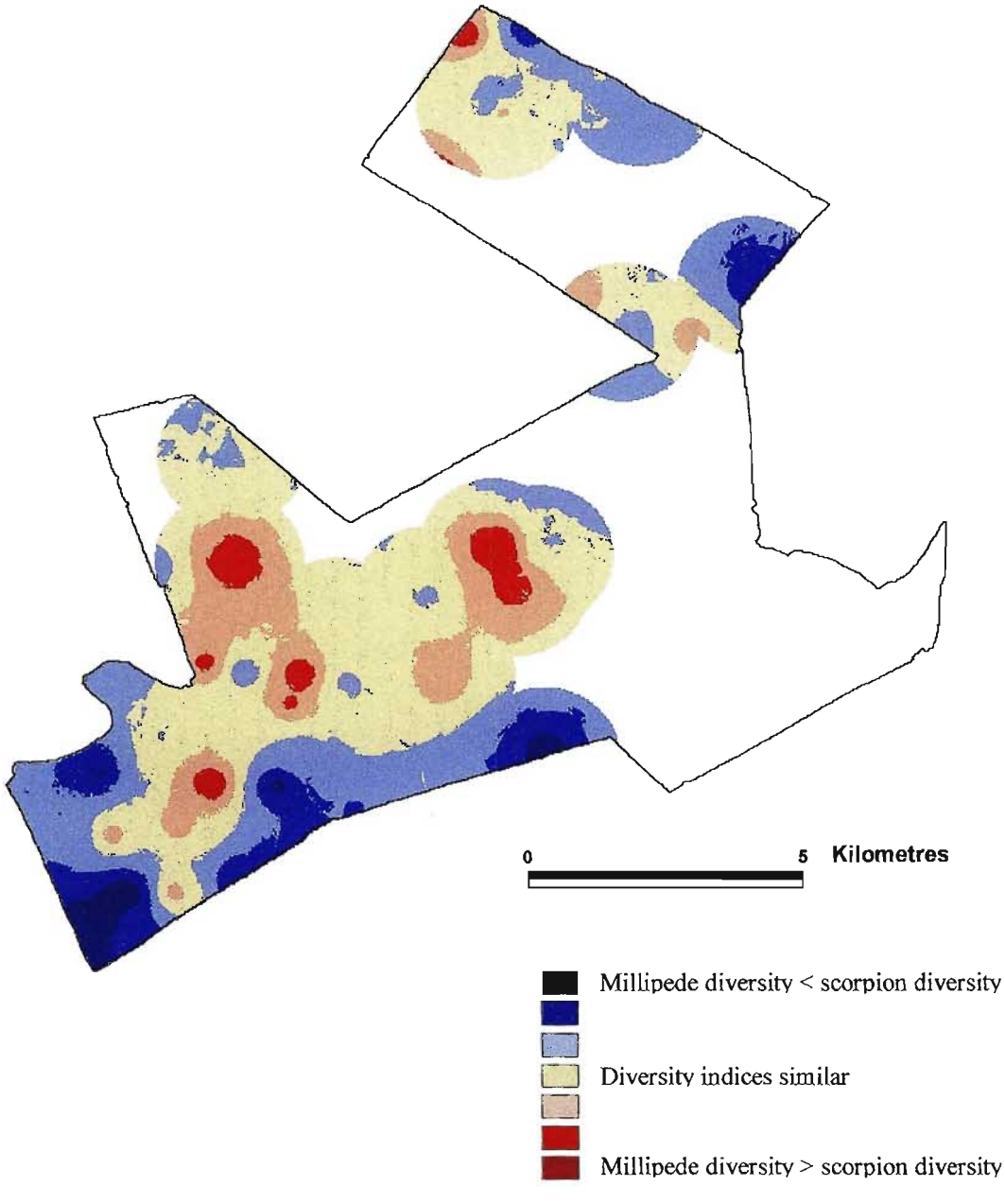


Figure 5.5. The difference in predicted diversity between millipede and scorpion groups.

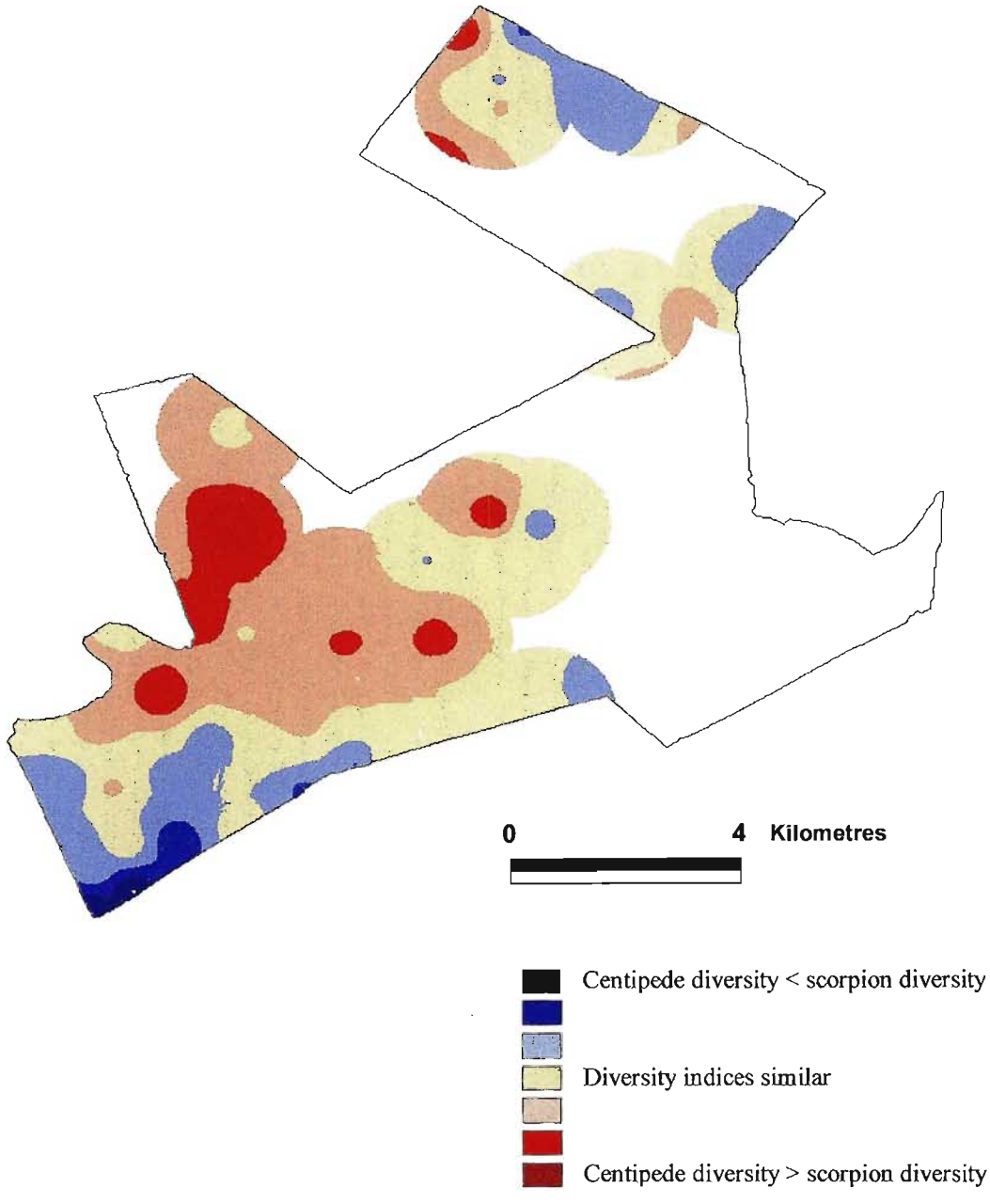


Figure 5.6. The difference in predicted diversity between centipede and scorpion groups.

Discussion

Millipede diversity was found to be related to a number of micro-habitat variables, many of which were associated with the vegetation. Vegetation density of the woody plants less than lm was the most important variable, followed by the variables relating to leaf litter cover. There was a positive relationship between these three variables and diversity, indicating that diversity increases with an increase in vegetation density, leaf cover and leaf thickness. Two of the five vegetation types were also found to influence the diversity of millipedes. Similar relationships have been found in other studies. Areas where there is a high diversity of plant species or where there is a closed canopy have been found to contain a high diversity of millipede species (Dangerfield & Telford, 1989; Hopkin & Read, 1992; Mwabvu, 1997). Litter standing crop and vegetation cover have also been found to influence millipede distribution (Tarasevich, 1992). Although litter cover and litter type have been shown to influence the distribution of millipedes (Bano, 1992; Kime, 1992), areas that contain a large accumulation of litter have, however, been shown to contain the lowest densities of millipedes (Kime, 1992).

Other factors that have been found to determine millipede distribution within habitats include soil depth (Tarasevich, 1992), soil texture, soil-water content, mineral content, temperature and humidity (Kime, 1992). Although many of these factors were sampled and used in the multiple regression analysis, they did not significantly contribute to the distribution of millipedes in this study. These relationships were demonstrated for the forest environment (Kime, 1992; Tarasevich, 1992) and may not hold for the savanna environment (this study).

However, other factors that have been found, in other studies, to influence the distribution of millipedes in the savanna environment were also not significant in this study. These factors include rocks, stones, fallen branches, deserted termite mounds or other debris is that can serve as a shelter against the heat and aridity (Lawrence, 1966; Lawrence, 1984). Lawrence (1966) also suggested that the dung of ruminants and other large herbivores may be an important micro-habitat factor as it is often used by millipedes as a suitable place for egg laying and the early larval stages after hatching (Lawrence, 1966). Although the presence and numbers of elephant dung balls were sampled, there was no significant relationship between them and the distribution of millipedes. The effect of some of these variables on millipede distribution may have been described base purely on observation without quantified sampling, with the result that a more quantified study produced different results.

All the micro-habitat variables that were found to significantly influence the distribution of centipedes were related to soil conditions and to moisture. The two variables with the greatest effect were soil moisture and rainfall. However, increasing rainfall had a negative effect on diversity, while soil moisture positively influenced diversity. This indicates that the moisture of the micro-habitat is an important consideration in the distribution of these organisms. The other variables were soil pH and rock cover. Rock cover would probably increase the attractiveness of a habitat in that centipedes use rocks for refuge (Lawrence, 1984). Other micro-habitat factors that have been suggested to influence centipede distribution through their potential as refuge sites include stones or logs (Lawrence, 1984). However, fallen branches were not found to significantly contribute to distribution in this multiple regression analysis. Data collected in Italy indicate that centipede distribution within habitats shows good correlation with habitat characteristics of certain vegetation types (Zapparoli, 1992a), however none of the vegetation variables were significant in determining centipede distribution in the Makalali data set.

Polis (1990b) states that scorpions are also not randomly distributed within a habitat, but that particular species are normally found in specific micro-habitats (Bridges, le Roux & van Aardt, 1997) either associated with the ground or vegetation (Polis, 1990b). The results from the multiple regression analysis for the Makalali data also confirmed that there are micro-habitat variables that determine the distribution of scorpions within a habitat. Scorpions were found to be significantly influenced by the soil pH and cations as well as air temperature, leaf litter thickness and the density of the vegetation less than 1m high. Other studies have also found that scorpion distribution and diversity is influenced by temperature, soil or rock characteristics, stone and litter cover and environmental physiognomy (Polis, 1990b). Soil characteristics may be important to certain scorpion species in that they may have specific soil types where they can construct burrows (Newlands, 1978; Polis, 1990b; Bridges *et.al*, 1997). Vegetation characteristics do not appear to have a strong effect on the distribution of scorpions. It has been suggested that vegetation may not be as important as other factors as there are some species that exhibit a high degree of plasticity (Polis, 1990a) and are not restricted to certain vegetation types, but rather live in several vegetation types (Polis, 1990b). A study by Margules, Milkovits & Smith (1994) found that there was a higher probability of finding scorpions on slopes rather than in drainage lines. However, in this analysis slope did not significantly influence the distribution of scorpions.

As the factors determining the distribution of organisms are heterogeneously distributed within the environment, so are the organisms. Because GIS techniques are able to divide up areas of

heterogeneous habitat into biologically meaningful subunits, they can be an important tool in ecological work (Haslett, 1990). Their use has, in the past focused on the vertebrates as opposed to the invertebrates. Studies have determined the habitat preferences of certain vertebrates and then used this information to predict suitable habitats or to provide a clearer understanding of the actual distribution (Haslett, 1990). Their relationship with environmental variables may be easier to determine and as a result areas that can provide a suitable habitat can be determined with greater ease than is the case with invertebrates. However, GIS techniques can also be important in invertebrate research because they can operate at various scales. The heterogeneous distribution of important micro-habitat variables within habitat types can be used to determine expected organism distribution within an environment. In this chapter, GIS has proved useful in modeling variation in different micro-habitat factors and using the relationship between the diversity and micro-habitat requirements of three focal groups, to predict diversity at a larger scale based on these relationships.

CHAPTER 6
SUMMARY & CONCLUDING REMARKS

This project had three main aims. The first was to determine effective and efficient sampling methods for millipedes, centipedes and scorpions in the savanna environment, the second to determine and describe any range in their distribution patterns between habitat types (local scale) in the Greater Makalali Conservancy and then finally to determine the processes influencing their distribution within these habitat types (micro-habitat scale).

In order to determine the best method for sampling millipedes, centipedes and scorpions in the savanna environment, the effectiveness and efficiency of six invertebrate sampling methods were tested. One of the important requirements in invertebrate sampling, especially since the inception of the Convention of Biological Diversity, is that sampling methods need to be rapid but effective. In this way a large amount of information on a group's distribution can be collected in the shortest possible time, while at the same time ensuring that most, if not all, species have been sampled. Sampling methods also need to be standardised in order to allow comparison of results between areas. This study found that in the savanna environment there are different sampling methods that are more effective and efficient for the three groups of organisms being studied. The drive transects and the sampling of $9m^2$ quadrats are the most efficient methods for sampling millipedes. These two methods sampled all the millipede species, some of which were only sampled using these methods. Centipedes were sampled most effectively by actively searching either nested or random quadrats. However, as the accumulation curve for the nested quadrats did not plateau at or before the largest area searched ($25m^2$) in the nested quadrats, the area that needs to be searched to effectively sample this group is not known. Almost all the scorpion individuals sampled were captured using the pitfall trap method. Although this method may not be very rapid, as the traps need to be set up and then left for a period of 2 weeks, it is the only method tested that will effectively sample this group.

Differences in the diversity of millipedes, centipedes and scorpions were observed between the five habitat types sampled. Heterogeneous habitats have been shown, in a number of studies, to contain a greater diversity of organisms (Utez, 1974; Greenstone, 1984; Dangerfield & Telford, 1992; Rosenzweig, 1996; Siemann, 1998) as they contain a higher number of micro-habitats which can support a larger number of species. However, although a higher diversity of millipedes, centipedes and scorpions was found in the more heterogeneous habitats (i.e. rocky outcrops), a greater number of species was often recorded in the homogeneous habitats. This

was seen in the mopane habitat, which contained the greatest number of millipede and scorpion species. The mopane habitat also contained millipede and scorpion species that were only found in that habitat type, as did the white sandy bushveld and general mixed bushveld in the case of scorpions. However, the rocky outcrop habitat type contained the highest millipede and centipede diversity and the second highest scorpion diversity. As a result, this study indicates that although heterogeneous habitats may support a high diversity, homogeneous habitat types may also be important conservation areas for these three invertebrate groups as they contain species that may not occur in more heterogeneous habitat types. This highlights the importance of understanding the particular habitat preferences of species or groups of organisms before they can be conserved.

As well as spatial differences in diversity between habitat types, differences in diversity between sampling periods were also investigated. Differences in diversity between sampling periods were demonstrated for millipedes and scorpions, however there was no significant difference in centipede diversity between the three sampling periods. The highest diversity for each focal group was recorded during the sampling undertaken in November 1999. This period was just after the start of the rainfall season.

One of the most important considerations in ecology is understanding the processes controlling diversity. As not much work has been done on processes determining millipede, centipede and scorpion diversity, especially within the savanna environment, this was the third aim of the project. Data on micro-habitat variables were collected and related to the diversity of each group of organisms. Some of the micro-habitat variables that were found to affect millipede diversity in the Greater Makalali Conservancy, match those found in other studies. Millipede diversity within the various habitat types was found to be positively correlated to the vegetation density of woody plants less than 1m tall, leaf litter cover and thickness and the *Combretum apiculatum – Terminalia prunoides* low closed woodland vegetation type. Centipede diversity was positively influenced by soil moisture and soil pH and negatively influenced by rock size and rainfall, while scorpion diversity was related to soil cations and pH, leaf litter depth and air temperature.

Due to the heterogeneous distribution of these important micro-habitat variables, both within a habitat and between different habitats, organisms dependent on these variables will also be distributed heterogeneously within and between habitat types. This has important conservation implications for these species. Knowing these relationships between micro-habitat variables and

these three invertebrate groups allows one to predict a possible diversity measure for these organisms in areas within the savanna environment where no sampling has taken place. This may allow one to determine areas that may be important to conserve as they may provide a good habitat for these groups of invertebrates. This could be at a local scale (i.e. within a particular reserve) or even at a larger scale, such as southern Africa.

In order to predict diversity in areas where no sampling has taken place based on the relationship between the diversity of groups of organisms and micro-habitat variables, one needs to know, accurately and at a small scale, the distribution of these variables throughout the area in question. As a result, Conservancy wide variables such as altitude, slope, aspect, rainfall and air temperature as well as micro-habitat variables such as soil characteristics were accurately measured and mapped using GIS. Using the relationships between each of the invertebrate focal groups and the micro-habitat variables, diversity for each group was predicted in areas in the Conservancy where no sampling had taken place.

The conservation of these groups of organisms will also need to take into consideration the influences of certain activities or organisms on these three invertebrate groups. Factors that negatively affect the processes driving the diversity of each of these groups will result in a decrease in the diversity of these three groups. However, although this study has determined a range of factors that influence the diversity of each of these groups, the effect of changes in these factors has not been documented. Elephants, fire or bush clearing by humans, for example, may reduce the density of woody plants that could then result in a decrease in the diversity of millipedes. However, as these effects on diversity have not been quantified, a large amount of research remains to be done on the processes and patterns in diversity and factors affecting the distribution of millipedes, centipedes and scorpions, before these relationships are fully understood.

This study has also highlighted, particularly through the high diversity of millipedes and scorpions, the importance of an environment that has, in the past, not been considered to be important for millipedes, centipedes or scorpions. The discovery of three millipede species that have not been described before and new distribution records for some of the species, also emphasises the importance of undertaking invertebrate diversity studies in the savanna environment.

REFERENCES

Addicott, J.F., Aho, J.M., Antolin, M.F., Padilla, D.K., Richardson, J.S. & Soluk, D.A., (1987) Ecological neighbourhoods: scaling environmental patterns, *Oikos*, **49**: 340-346

Ausden, M., (1997) Invertebrates. In Sutherland, W.J. (ed), Ecological census techniques, Cambridge University Press, Cambridge, pp 139-178

Balmford, A. & Gaston, K.J., (1999) Why biodiversity surveys are good, *Nature*, **398**: 204-205

Bano, K., (1992) The role of the millipede *Jonespeltis splendidus* Verhoeff in an ecosystem, *Ber. Nat.-mad. Verein Innsbruck*, **10**: 327-331

Barr, D. & Carter, W.M., (1995) Mapping biodiversity, *Rotunda*, 34-39

Beardall, G.M., Joubert, S.C.J. & Retief, P.F., (1984) An evaluation of the use of correspondence analysis for the analysis of herbivore-habitat selection, *S. Afr. J. Wildl. Res.*, **14**: 79-88

Beccaloni, G.W. & Gaston, K.J., (1995) Predicting the species richness of neotropical forest butterflies: Ithomiinae (Lepidoptera: Nymphalidae) as indicators, *Biological Conservation*, **71**: 77-86

Beck, M.W., (1998) Biodiversity: A concept lost in the mist between ecology and conservation biology. In Lunney, D., Dawson, T. & Dickman, C.R. (eds) Is the biodiversity tail wagging the zoological dog?, Transactions of the Royal Zoological Society of New South Wales, Mosman, Australia

Bezuidenhout, H., (1995) An ecological study of the major vegetation communities of the Vaalbos National Park, Northern Cape. 2. The Graspan-Holpan section, *Koedoe*, **38**: 65-83

Biodiversity Series 1, (1993) Biodiversity Unit, Department of the Environment, Sport and Territories, Commonwealth of Australia

Black, D.G., (1997) Diversity and biogeography of Australian millipedes (Diplopoda), Memoirs of the Museum of Victoria, **56**: 557-561

Bredenkamp, G.J., Theron, G.K. & van Vuuren, D.R.J., (1983) Ecological interpretation of plant communities by classification and ordination of quantitative soil characteristics, *Bothalia*, **14**: 691-699

Brennan, K.E.C., Majer, J.D. & Reygaert, N., (1999) Determination of an optimal pitfall trap size for sampling spiders in a Western Australian Jarrah forest, *Journal of Insect Conservation*, **3**: 297-307

Bridges, C.R., le Roux, J.M. & van Aardt, W.J., (1997) Ecophysiological adaptions to dry thermal environments measured in two unrestrained Namibian scorpions *Parabuthus villosus* (Buthidae) and *Opisthophthalmus flavescens* (Scorpionidae), *Physiological Zoology*, **70**: 244-256

Brown, L.R. & Bredenkamp, G.J., (1994) The phytosociology of the southern section of Borakalalo Nature Reserve, *Koedoe*, **37**: 59-72

Brown, L.R., Bredenkamp, G.J. & van Rooyen, N., (1995) The phytosociology of the western section of Borakalalo Nature Reserve, *Koedoe*, **38**: 49-64

Brown, L.R., Bredenkamp, G.J. & van Rooyen, N., (1996) The phytosociology of the northern section of the Borakalalo Nature Reserve, *Koedoe*, **39**: 9-24

Brussard, L., Behan-Pelletier, V.M., Bignell, D.E., Brown, V.K., Didden, W., Folgarait, P., Fragoso, C., Freckman, D.W., Gupta, V.V.S.R., Hattori, T., Hawksworth, D.L., Klopatek, C., Lavelle, P., Malloch, D.W., Rusek, J., Soderstrom, B., Tiedje, J.M. & Virginia, R.A., (1997) Biodiversity and ecosystem functioning in soil, *Ambio*, **26**: 563-570

Bullock, J., (1996) Plants. In Sutherland, W.J. (ed) Ecological census techniques, Cambridge University Press, Cambridge, pp 111-139

Bush, M.B., (1997) Ecology of a changing planet, Prentice Hall, New Jersey

Churchill, T.B. & Arthur, M.J., (1999) Measuring spider richness: effects of different sampling methods and spatial and temporal scales, *Journal of Insect Conservation*, **3**: 287-295

Colwell, R.K. & Coddington, J.A., (1994) Estimating terrestrial biodiversity through extrapolation, *Phil. Trans. R. Soc.Lond.*, **345**: 101-118

Cooper, A.B. & Millspaugh, J.J., (1999) The application of discreet choice models to wildlife resource selection studies, *Ecology*, **80**: 566-575

Crawley, M.J., (1993) GLIM for ecologists, Blackwell Scientific Publications, Oxford

Cumming, D.H.M., (1982) The influence of large herbivores on savanna structure in Africa. In Huntley, B.J. & Walker, B.H. (eds) Ecology of tropical savannas, Springer-Verlag, Berlin

Dangerfield, J.M., (1990) Abundance, biomass and diversity of soil macrofauna in savanna woodland and associated managed habitats, *Pedobiologia*, **34**: 141-150

Dangerfield, J.M. & Kaunda, S.K., (1994) Millipede behaviour in a savanna woodland habitat in south-east Botswana, *Afr. J. Ecol.*, **32**: 337-341

Dangerfield, J.M. & Telford, S.R., (1989) Are millipedes important for soil fertility?, *The Zimbabwe Science News*, **23**: 66-68

Dangerfield, J.M. & Telford, S.R., (1991) Seasonal activity patterns of Julid millipedes in Zimbabwe, *Journal of Tropical Ecology*, 7: 281-285

Dangerfield, J.M. & Telford, S.R., (1992) Species diversity of Julid millipedes: between habitat comparisons within the seasonal tropics, *Pedobiologia*, **36**: 321-329

Dekker, B., van Rooyen, N. & Bothma, J. du P., (1996) Habitat partitioning by ungulates on a game ranch in the Mopani veld, *S. Afr. Wildl. Res.*, **26**: 117-122

DeVries, P.J., Walla, T.R. & Greeney, H.F., (1999) Species diversity in spatial and temporal dimensions of fruit-feeding butterflies from two Ecuadorian rainforests, *Biological Journal of the Linnean Society*, **68**: 333-353

Eastwood, E.B., (1978) Some observations on the distribution and biology of scorpions on Table Mountain, *Ann. S. Afr. Mus.*, **74**: 229-248

Edwards, D., (1983) A broad-scale structural classification of vegetation for practical purposes, *Bothalia*, **14**: 705-712

Ehrlich P.R., & Wilson, E.O., (1991) Biodiversity studies and policy, *Science*, **253**: 758-762

Fabricus, C. & Coetzee, K., (1992) Geographic information systems and artificial intelligence for predicting the presence or absence of mountain reedbuck, *S. Afr. J. Wildl. Res.*, **22**: 80-85

Faith, D.P. & Walker, P.A., (1996) How do indicator groups provide information about the relative biodiversity of different sets of areas?: on hotspots, complementarity and pattern-based approaches, *Biodiversity letters*, **3**: 18-25

Gaston, K.J., (2000) Global patterns in biodiversity, *Nature*, **405**: 220-227

Goodman, P.S., (1990) Soil, vegetation and large herbivore relations in Mkuzi Game Reserve, Natal, PhD Thesis, University of the Witwatersrand, Johannesburg

Goodman, S.M. & Lanyon, S.M., (1994) Scientific collecting, *Conservation Biology*, **8**: 314-315

Greenstone, M.H., (1984) Determinants of web spider species diversity: vegetation structural diversity vs. prey availability, *Oecologia*, **62**: 299-304

Groombridge, B., (1992) Global biodiversity: Status of the earth's living resources, Chapman and Hall, London

Hamer, M.L., (1997) A preliminary assessment of the southern African millipede fauna: diversity and conservation (Diplopoda), *Ent. scand. Suppl.*, **51**: 209-217

Hamer, M.L., (1998) Checklist of southern African millipedes, *Annals of the Natal Museum*, **39**: 11-82

Hamer, M.L., (1999) An illustrated guide to the spirostreptidan (Diplopoda: Spirostreptida) genera of southern Africa, *Annals of the Natal Museum*, **40**: 1-22

Hamer, M.L. & Slotow, R., (in press) Patterns of speciation and distribution in southern African *Doratogonus* (Diplopoda: Spirostreptidae), *Fragmenta Faunistica*, **40**

Harington, A., (1978) Burrowing biology of the scorpion *Cheloctonus jonesii* Pocock (Scorpionida, Scorpionidae), *The Journal of Arachnology*, **5**: 243-249

Haslett, J.R., (1990) Geographic information systems: A new approach to habitat definition and the study of distributions, *TREE*, **5**: 214-218

Hill, M.O., (1994) DECORANA and TWINSPAN, for ordination and classification of multivariate species data: a new addition with supporting programs, in Fortran 77, Huntington: Institute of Terrestrial Ecology, England

Hodgson, J.M., (1976) Soil survey field handbook. Describing and sampling soil samples, Bartholomew Press, Dorking

Hopkin, S.P. & Read, H.J., (1992) The biology of millipedes, Oxford University Press, New York

Ives, A.R., Gross, K. & Klug, J.L. (1999) Stability and variability in competitive communities, *Science*, **286**: 542-544

Judas, M. & Hauser, H., (1998) Patterns of isopod distribution: from small scale to large scale, *Israel Journal of Zoology*, **44**: 333-343

Kadmon, R. & Heller, J., (1998) Modelling faunal responses to climatic gradients with GIS: land snails as a case study, *Journal of Biogeography*, **25**: 527-539

Kime, R.D., (1992) On abundance of west-European millipedes, *Ber. Nat.-mad. Verein Innsbruck*, **10**: 393-399

Kime, R.D. & Golovatch, S.I., (2000) Trends in the ecological strategies and evolution of millipedes (Diplopoda), *Biological Journal of the Linnean Society*, **69**: 333-349

Klinger, K., (1992) Diplopods and Chilopods of conventional and alternative (biodynamic) fields in Hesse (FRG), *Ber. Nat.-mad. Verein Innsbruck*, **10**: 243-250

Kos, I., (1992) A review of the taxonomy, geographical distribution and ecology of the centipedes of Yugoslavia, *Ber. Nat.-mad. Verein Innsbruck*, **10**: 353-360

Krebs, C.J., (1989) Ecological Methodology, Harper & Row, New York

Lamoral, B.H., (1979) The scorpions of Namibia, *Annals of the Natal Museum*, **23**: 504-528

Lawrence, R.F., (1955) Scorpions. In. South African Animal Life (Lund University Expedition), **1**: 205-259

Lawrence, R.F., (1964) The solifugae, scorpions and pedipalpi of the Kruger National Park, *Koedoe*, **7**: 30-39

Lawrence, R.F., (1966) The Myriapoda of the Kruger National Park, *Zoologica Africana*, **2**: 225-262

Lawrence, R.F., (1967) Supplementary list of the Solifugae, scorpions and pedipalpi of the Kruger National Park, *Koedoe*, **10**: 82-86

Lawrence, R.F., (1984) Centipedes and millipedes of southern Africa, A.A. Balkema, Cape Town

Longino, J.T., (1994) How to measure arthropod diversity in a tropical rainforest, *Biology International*, **28**: 3-13

Low, A.B. and Rebelo, A.G., (eds) (1996) Vegetation of South Africa, Lesotho and Swaziland, Department of Environmental Affairs and Tourism, Pretoria

Ludwig, R.A. & Reynolds, J.F., (1988) Statistical Ecology, John Wiley & Sons

Luff, M.L., (1975) Some features influencing the efficiency of pitfall traps, *Oecologia*, **19**: 345-357

Madari, B., Kiss, I. & Korsos, Z., (1996) Community-structure parameters of millipedes (Diplopoda) in five different habitats, *Annales Historico-Naturales Musei Nationalis Hungarici*, **88**: 79-87

Majer, J.D., (1997) The use of pitfall traps for sampling ants – A critique, *Memoirs of the Museum of Victoria*, **56**: 323-329

Margules, C.R., Milkovits, G.A. & Smith, G.T., (1994) Contrasting effects of habitat fragmentation on the scorpion *Cerophonius squama* and an amphipod, *Ecology*, **75**: 2033-2042

McCann, K.S., (2000) The diversity-stability debate, *Nature*, **405**: 228-233

McGeoch, M.A., (1998) The selection, testing and application of terrestrial insects as bioindicators, *Biol.Rev.*, **73**: 181-201

Melborne, B.A., Gullan, P.J. & Su, Y.N., (1997) Interpreting data from pitfall trap surveys: Crickets and slugs in exotic and native grasslands of the Australian Capital Territories, *Memoirs of the Museum of Victoria*, **56**: 361-367

Melton, D.A., (1987) Habitat selection and resource scarcity, *South African Journal of Science*, **83**: 646-651

Menge, B.A. & Olson, A.M., (1990) Role of scale and environmental factors in regulation of community structure, *TREE*, **5**: 52-57

Merrill, T., Mattson, D.J., Wright, R.G. & Quigley, H.B., (1999) Defining landscapes suitable for restoration of grizzly bears *Ursus arctos* in Idaho, *Biological Conservation*, **87**: 231-248

Mesibov, R., Taylor, R.J.& Brereton, R.N., (1995) Relative efficiency of pitfall trapping and hand-collecting from plots for sampling of millipedes, *Biodiversity and Conservation*, **4**: 429-439

Michelmore, F., (1994) Keeping elephants on the map: Case studies of the application of GIS for conservation. In Miller, R.I., (ed) Mapping the diversity of nature, Chapman & Hall, London

Mladenoff, D.J. & Sickley, T.A., (1998) Assessing potential Gray Wolf restoration in the northeastern United States: A spatial prediction of favourable habitat and potential population levels, *J. Wildl. Manage.*, **62**: 1-10

Mueller-Dombois, D. & Ellenberg, H., (1974) Aims and methods of vegetation ecology, John Wiley & Sons, New York

Munthali, S.M. & Banda, H.M., (1992) Distribution and abundance of the common ungulates of Nyika National Park, Malalwi, *Afr. J. Ecol.*, **30**: 203-212

Mwabvu, T., (1997) Millipedes in small-scale farming systems in Zimbabwe: abundance and diversity (Diplopoda, Spirostreptida), *Ent. scand. Suppl.*, **51**: 287-290

Myers, N., Miltermeier, R.A., Miltermeier, C.G., da Fonseca, G.A.B. & Kent, J., (2000) Biodiversity hotspots for conservation priorities, *Nature*, **403**: 853-858

Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H. & Woodfin, R.M., (1994) Declining diversity can alter the performance of ecosystems, *Nature*, **368**: 734-736

Newlands, G., (1972) Ecological adaptations of Kruger National Park Scorpionids (Arachnida: Scorpionides), *Koedoe*, **15**: 37-48

Newlands, G., (1973) The scorpions of Namibia (Arachnida: Scorpionida), *Annals of the Natal Museum*, **23**: 497-784

Newlands, G., (1978) Review of southern African scorpions and scorpionism, *SA Medical Journal*, **54**: 613-615

Oliver, I. & Beattie, A.J., (1996) Designing a cost-effective invertebrate survey: a test of methods for rapid assessment of biodiversity, *Ecological Applications*, **6**: 594-607

Pearce, D., & Moran, D., (1994) The economic value of biodiversity, Earthscan Publications, London

Pienaar, U.D.V., (1991) An overview of conservation in South Africa and future perspectives, *Koedoe*, **34**: 73-80

Pooley, E. (1994) The complete field guide to trees of Natal, Zululand and Transkei, Natal Flora Publications Trust, Durban

Polis, G.A., (1990b) Ecology. In Polis, G.A. (ed), The biology of scorpions, Stanford University Press, Stanford

Polis, G.A., (1990a) Introduction. In Polis, G.A. (ed), The biology of scorpions, Stanford University Press, Stanford

Prendini, L., (in press) A review of synonymy and subspecies in the genus *Opistophthalmus* C.L. Koch (Scorpiones: Scorpionidae), *African Entomology*

Purvis, A. & Hector, A., (2000) Getting the measure of biodiversity, *Nature*, **405**: 212-219

Reid, W.V. and Miller, K.R., (1989) Keeping options alive: the scientific basis for conserving biodiversity, *WRI Publications Brief*, Washington D.C.

Rodriguez, J.P., Pearson, D.L. & Barrera, R.R., (1998) A test for the adequacy of bioindicator taxa: Are tiger beetles (Coleoptera: Cicindelidae) appropriate indicators for monitoring the degradation of tropical forests in Venezuela?, *Biological Conservation*, **83**: 69-76

Rosenberg, D.M., Danks, H.V. & Lehmkuhl, D.M., (1986) Importance of insects in environmental impact assessment, *Environmental management*, **10**: 773-783

Rosenzweig, M.L., (1996) Species diversity in space and time, Cambridge University Press, Cambridge

Samways, M.J., (1993) Insects in biodiversity conservation: some perspectives and directives, *Biodiversity and Conservation*, **2**: 258-282

Samways, M.J., (1994) Insect conservation biology, Chapman & Hall, London

Sanderson, R.A., Rushton, S.P., Cherrill, A.J. & Byrne, J.P., (1995) Soil, vegetation and space: an analysis of their effects on the invertebrate communities of a moorland in north-east England, *Journal of Applied Ecology*, **32**: 506-518

Scholes, R.J., (1997) Savanna. In Cowling, R.M., Richardson, D.M. and Pierce, S.M. (eds) Vegetation of southern Africa, Cambridge University Press, Cambridge, pp 258-278

Scholes, R.J. and Walker, B.H., (1993) An African savanna: Synthesis of the Nylsvley study, Cambridge University Press, Cambridge

Scogings, P.F., Theron, G.K. & Bothma, J. du P., (1990) Two quantitative methods of analysing ungulate habitat data, *S. Afr. J. Wildl. Res.*, **20**: 9-13

Shear, W.A., (1999) Millipeds, *American Scientist*, **87**: 232-239

Siemann, E., (1998) Experimental tests on effects of plant productivity and diversity on grassland arthropod diversity, *Ecology*, **79**: 2057-2070

Sissom, W.D., Polis, G.A. & Watt, D.D., (1990) Field and laboratory methods. In Polis, G.A. (ed), The biology of scorpions, Stanford University Press, Stanford

Slotow, R. & Hamer, M., (2000) Biodiversity research in South Africa: comments on current trends and methods, *South African Journal of Science*, **96**: 222-224

Southwood, T.R.E., (1991) Ecological methods, Chapman and Hall, London

StatSoft Inc., (1999). STATISTICA for Windows (Computer program manual), Tulsa

Stuart-Hill, G.C. & Tainton, N.M., (1999) Savanna. In Tainton, N.M. (ed) Veld management in South Africa, University of Natal Press, Pietermaritzburg, pp 312-316

Tainton, N.M., (1999) The savanna biome. In Tainton, N.M. (ed) Veld management in South Africa, University of Natal Press, Pietermaritzburg, pp 33-36

Tarasavich, Y.L., (1992) Diplopoda in the associations of mixed forests, *Ber. Nat.-mad. Verein Innsbruck*, **10**: 213-218

Tilman, D., (1999) The ecological consequences of changes in biodiversity: a search for general principles, *Ecology*, **80**: 1455-1474

Tilman, D., (2000) Causes, consequences and ethics of biodiversity, *Nature*, **405**: 208-211

Topping, C.J. & Sunderland, K.D., (1992) Limitations to the use of pitfall traps in ecological studies exemplified by a study of spiders in a field of winter wheat, *Journal of Applied Ecology*, **29**: 485-491

Trueman, J.W.H. & Cranston, P.S., (1997) Prospects for the rapid assessment of terrestrial invertebrate biodiversity, *Memoirs of the Museum of Victoria*, **56**: 349-354

Utez, G.W., (1979) The influence of variation in litter habitats on spider communities, *Oecologia*, **40**: 29-42

van Jaarsveld, A.S. & Chown, S.L. (1996) Strategies and time frames for implementing the Convention on Biological Diversity: Biological requirements, *South African Journal of Science*, **92**: 459-464

van Rooyen, N., Grunow, J.O. & Theron, G.K., (1989) Veld management. In Bothma, J. Du P., (ed) Game Ranch Management, J.L. van Schaik, Pretoria

van Rooyen, N. & Theron, G.K., (1989) Vegetation, veld types and game ranching regions of South Africa. In Bothma, J. Du P., (ed) Game Ranch Management, J.L. van Schaik, Pretoria

van Wyk, B & van Wyk, P., (1997) Field guide to trees of southern Africa, Struik Publishers, Cape Town

Walker, B.H., (1976) An approach to the monitoring of changes in the composition and utilisation of woodland and savanna vegetation, *S.Afr.J.Wild.Res.*, **6**: 1-32

Warburg, M.R., (1997) Biogeographic and demographic changes in the distribution and abundance of scorpions inhabiting the Mediterranean region in northern Israel, *Biodiversity and Conservation*, **6**: 1377-1389

Ward, D., Olsvig-Whittaker, L., Lawes, M., (1993) Vegetation-environment relationships in a Negev Desert erosion cirque, *Journal of Vegetation Science*, **4**: 83-94

Warrick, G.D. & Cypher, B.L., (1998) Factors affecting the spatial distribution of San Joaquin Kit foxes, *J. Wildl. Manage.*, **62**: 707-717

Whateley, A. & Porter, R.N., (1983) The woody vegetation communities of Hluhluwe-Corridor-Umfolozi Game Reserve Complex, *Bothalia*, **14**: 745-758

White, C., (1999) The vegetation ecology of the Newington region of Mpumalanga: A landscape ecology perspective, MSc thesis, University of Natal, Durban

White Paper on Biodiversity, Government Gazette, **385**: 23 July 1997

Williams, P.H. & Gaston, K.J., (1994) Measuring more of biodiversity: can higher taxon richness predict wholesale species richness, *Biological Conservation*, **67**: 211-217

Wytwer, J., (1992) Chilopoda communities of the fresh pine forests of Poland, *Ber. Nat.-mad. Verein Innsbruck*, **10**: 205-211

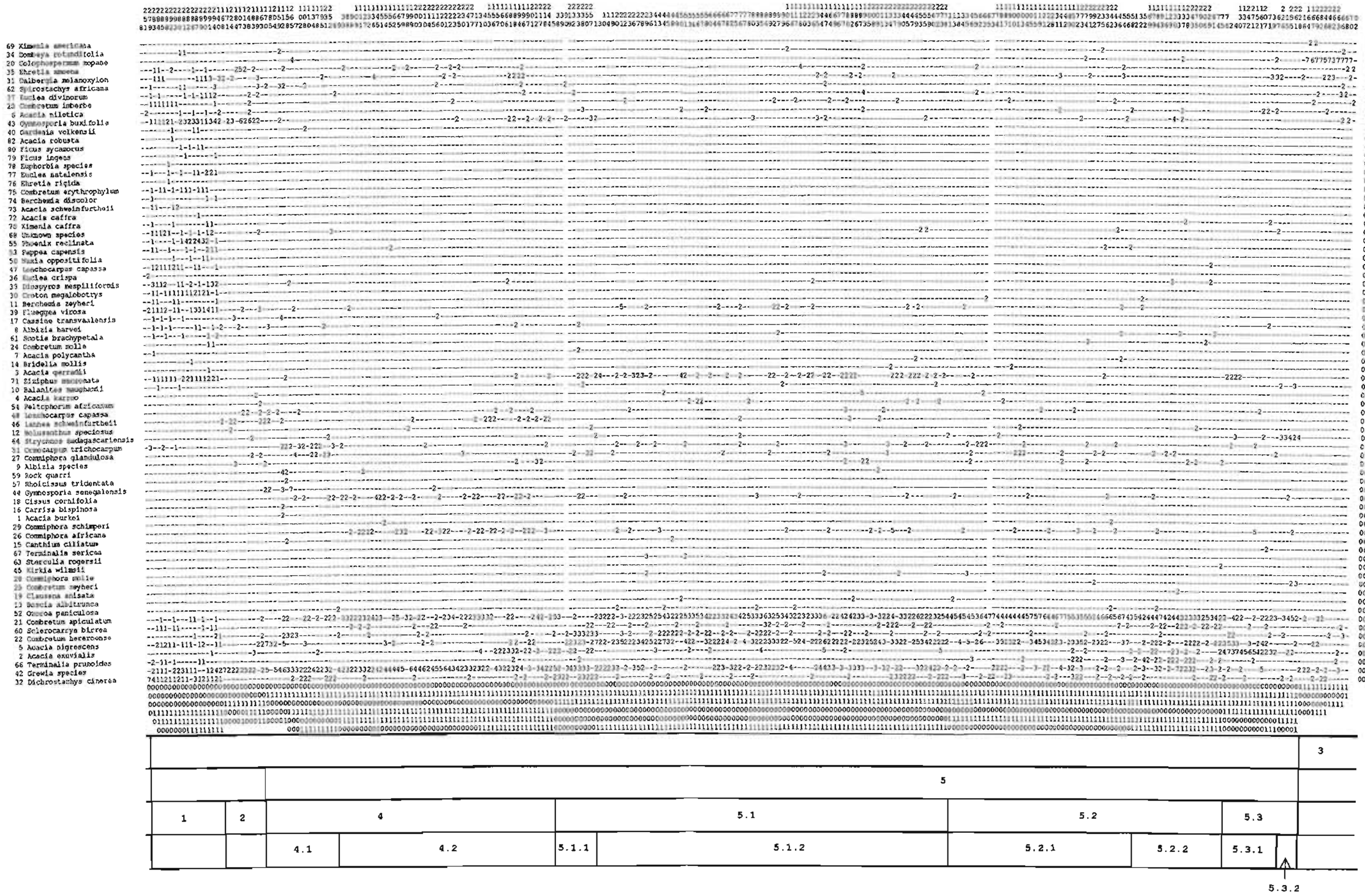
Yonzon, P., Jones, R. and Fox, J., (1991) Geographic information systems for assessing habitat and estimating population of Red Pandas in Langtang National Park, Nepal, *Ambio*, **20**: 285-288

Zapparoli, M., (1992a) Preliminary data on centipede communities of *Quercetea ilicis* and *Fatetalia sylvaticae* in central Italy, *Ber. Nat.-mad. Verein Innsbruck*, **10**: 197-204

Zapparoli, M., (1992b) Centipedes in urban environments: Records from the city of Rome (Italy), *Ber. Nat.-mad. Verein Innsbruck*, **10**: 231-236

Zar, J.H., (1999) Biostatistical analysis, Prentice Hall, New Jersey

Appendix A. The complete TWINSPAN ordered two-way output table for the Greater Makalali Conservancy.
Numbers 1 to 5.3.2 refer to the vegetation types (see text) and numbers 1-6 represent density values (see Table 2.1).
Numbers above the table refer to the transect numbers and the numbers beneath the table are the hierarchical classification assigned by TWINSPAN.



Appendix B. Checklists for millipedes, centipedes and scorpions recorded in the Greater Makalali Conservancy. These were compiled from literature and used to determine which species were regional specialists or generalists.

Millipede Checklist

Checklist compiled from Lawrence (1966), Hamer (1997), Hamer (1998) and Hamer & Slotow (in press).

Order: **SPIROSTREPTIDA**

Family: Spirostreptidae

Doratogonus flavifilis (Peters, 1855)

Distribution:

RSA: KNP: Orpen dam; Tshokwane; Mlondozi dam; Olifants-kamp; Napi road near Skukuza; Pafuri; Olifantspoort area; Letaba camp; Sabipoort. KZN: Hluhluwe Game Reserve; Umfolozi, Mseleni. Mpumalanga: Nelspruit. Northern Province: Makalali Private Game Reserve
Mozambique: Cabaceira Peninsula; Chai Chai (Masiene).
Zimbabwe: Haroni River; Umtali.
Zambia.

Doratogonus rugifrons (Attems, 1922)

Distribution:

RSA: Northern Province: Soutpansberg; Magoebaskloof; Tzaneen; Louis Trichardt; Makalali Private Game Reserve. North West Province: Pilanesberg Game Reserve
Namibia: Okahandja; Otjituo; Swakopmund; Windhoek; Zoekmekaar (all 1928).

Lophostreptus ulopygus Attems, 1928

Distribution:

RSA: Mpumalanga: Barberton; Kaapmuiden. Northern Province: Pietersburg; Makalali Private Game Reserve. North West Province: Venterskroon.

***Triaenostreptus* sp. A**

Distribution:

RSA: Northern Province: Makalali Private Game Reserve

Family: Harpagophoridae

Zinophora similis (Carl, 1917)

Distribution:

RSA: Gauteng: Sibasa district farm, Shewasaulu. KNP: Pafuri; Pretoriuskop; Punda Maria; Skukuza. Mpumalanga: Komatipoort, Sabipoort. Northern Province: Pietersburg; Lekgalameestse Nature Reserve; Ben Lavin Nature Reserve; Makalali Private Game Reserve.
Mozambique: Masiene near Chai Chai; Rikatla.

Family: Odontopygidae

Chaleponcus acanthoporus Attems, 1928

Distribution:

RSA: Northern Province: Messina; Makalali Private Game Reserve.

Spinotarsus colosseus (Attems, 1928)

Distribution:

RSA: KNP: Pumbe picket; Skukuza, Napi Rd. KZN: Hluhluwe Game Reserve. Northern Province: 20 miles east of Pietersburg, Makalali Private Game Reserve.

Spinotarsus **sp. A** (close or equal to *Spinotarsus modestus* (Attems; 1928))
Distribution:

RSA: Northern Province: Makalali Private Game Reserve.
Mozambique: Chai Chai.

Spinotarsus **sp. B**

Distribution:

RSA: Northern Province: Makalali Private Game Reserve

Order: **POLYDESMIDA**

Family: Dalodesmida

Gnomeskelus **(subgenus** ***Pristomeskelus*****) sp.**

Distribution:

RSA: Northern Province: Makalali Private Game Reserve

Order: **SPHAEROTHERIIDA**

Sphaerotherium modestum Attems, 1928

Distribution:

RSA: KNP: Mukutwanine koppies; Msimbit Forest; 2 miles south of Pafuri; Saselandongapoort; Skukuza (identification uncertain). Northern Province: Soutpansberg district; 20 miles east of Pietersburg, Makalali Private Game Reserve

***Sphaerotherium* sp. A**

Distribution:

RSA: Northern Province: Makalali Private Game Reserve

Centipede checklist

Checklist compiled from Lawrence (1955) and Lawrence (1966).

Order: **SCOLOPENDRAMORPHA**

Scolopendra moristans Linne., 1758

Distribution:

RSA: Cape Province: 15 miles S of Middleton. KNP: Talamati; Hapi area; Pafuri; Letaba Camp; Hlangulene; Nyanda sandveld; Machuluane Hills; Dongatziba; Punda Milia area; between Mahlakuza and Malonga; between Saselandongapoort and Pafuri; between Saselandongapoort and Mahlakuza; Leeu Pan; Skukuza. KZN: Gollel. Northern Province: Makalali Private Game Reserve.
Lesotho: Teyateyaneng, 18 miles NE of Maseru.
Namibia: Anabib; Sanitatas, Kowares; Kaoko-Otavi (all in the Kaokoveld).
Zimbabwe: West Nicholson.

Common in southern Africa except KZN and the extreme south west Cape.

Scolopendra sp.

Distribution:

RSA: Northern Province: Makalali Private Game Reserve.

Ethmostigmus trigonopodus (Leach, 1817)

Distribution:

RSA: KNP: Klopperfontein; Skukuza Camp; Shingwedzi; Malelane Rest Camp; Pretoriuskop; between Saselandongapoort and Mahlakuza eastern boundary. Northern Province: Gravelotte Railway Station; Makalali Private Game Reserve. Mpumalanga: Hectorspruit; Malelane. Transvaal (new provinces not known): Leydsdorp; Vygeboompoort.
Zimbabwe: Salisbury; Bulawayo; Umtali; Matebeleland; Bindura; Insiza; Victoria falls

Order: **GEOPHILOMORPHA**

Orphanaeus brevilabiatus Newport, 1845

Distribution:

RSA: KNP: confluence of the Sand and Sabi rivers; Hapi Dam area; Pafuri; Shingwedzi; Matukwane; Olifantspoort area in Msimbit forest; Malelane camp; Nhlanganinespruit; Mahlakuza pan; Pretoriuskop; Godleni; Eastern boundary; Sabipoort; Lower Sabi; Malelane camp; Leeu pan. Northern Province: Messina; Makalali Private Game Reserve.
Zimbabwe: West Nicholson; Victoria Falls, Livingstone.

Scorpion checklist

Checklist compiled from Lawrence (1955), Lawrence (1964), Lawrence (1967), Newlands (1972), Newlands (1973), Harington (1978) and Prendini (in press).

Family: Buthidae

Parabuthus transvaalicus Purcell 1899

Distribution:

RSA: KNP: Letaba Camp; Nuwe Oliphants Kamp; Tshokwane; Hapi pool; Pafuri; Oliphantspoort; Msimbit Forest; Shingwedzi; Mahlakuza pan; Malonga; Punda Milia; Godleni near Krokodilbrug; Eastern boundary; Lower Sabi. Northern Province: Makalali Private Game Reserve.
Zimbabwe: 30 miles N Beit Bridge

Parabuthus mossambicensis

Distribution:

RSA: Northern Province: Makalali Private Game Reserve

Uroplectus carinatus Pocock

Distribution:

RSA: KNP: Shaben Kop; Olifants area; Lower Sabi. Northern Province: Makalali Private Game Reserve

Uroplectus olivaceus Pocock, 1896

Distribution:

RSA: KNP: Sabi River near Skukuza; Pafuri; Nyandu Sandveld; Timisini fontein; Tshokwane; Oliphantspoort; Msimbit forest; Leeupan between Tshokwana and Letaba (1950-1951); Malelane Rest Camp; Lower Sabi; Godleni near Krokodilbrug; Gomondwane; Hippo Pool near Krokodilbrug; Eastern boundary; Sabi poort. Northern Province: Makalali Private Game Reserve.

Family: Scorpionidae

Cheloctonus jonesi Pocock, 1892

Distribution:

RSA: KNP: near Madziringwe mouth, Faai plots; Malelane Rest Camp; Nyandu Sandveld; Pumbe picket; Punda Milia; Gomondwane. Northern Province: Makalali Private Game Reserve; Newington
KZN: Pongola
Mozambique
Swaziland
Zimbabwe

Hadogenes troglodytes (Peters, 1861)

Distribution:
RSA: KNP: Napi Dam; Hapi kop; Pafuri; Olifantspoort; Timisini fontein; Balule Kamp; Nuwe Olifants Kamp; Matilolo. Northern Province: Makalali Private Game Reserve
Mozambique: Tette

Opisthacanthus asper

Distribution:
RSA: Northern Province: Makalali Private Game Reserve

Opistopthalmus boehmei (Pocock, 1899)

Distribution:
RSA: KNP: Northern tip of the park; Saselandonga poort; Punda Milia. Northern Province: N of the Zoutpansberg; Makalali Private Game Reserve

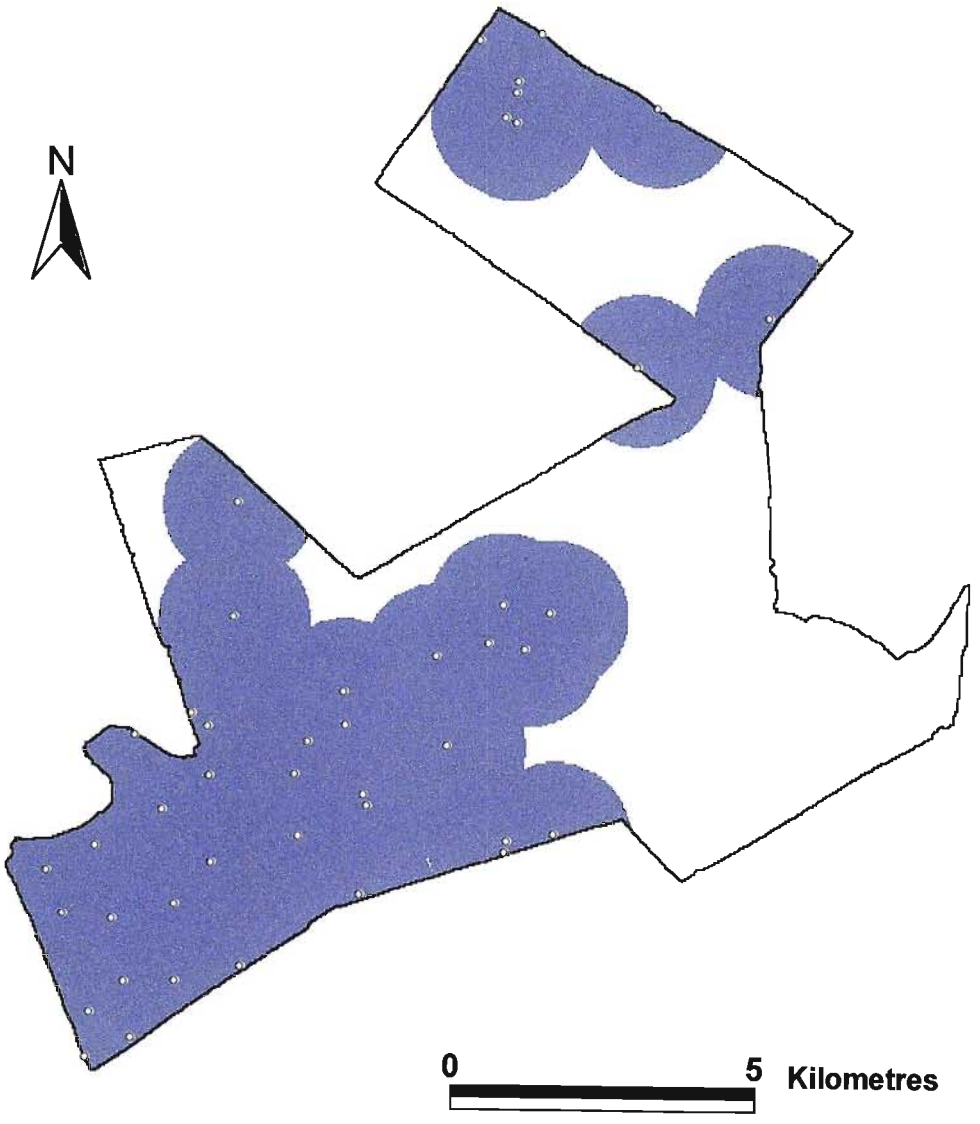
Opistopthalmus glabrifrons Peters, 1861

Distribution:
RSA: KNP: Skukuza; Dongadziba; Lower Sabi river road; Shingwedzi; between Saselandonga poort and Mahlakuza; Punda Milia; Malelane Rest Camp; Gomondwane. Northern Province: Makalali Private Game Reserve.
Mozambique: Tette

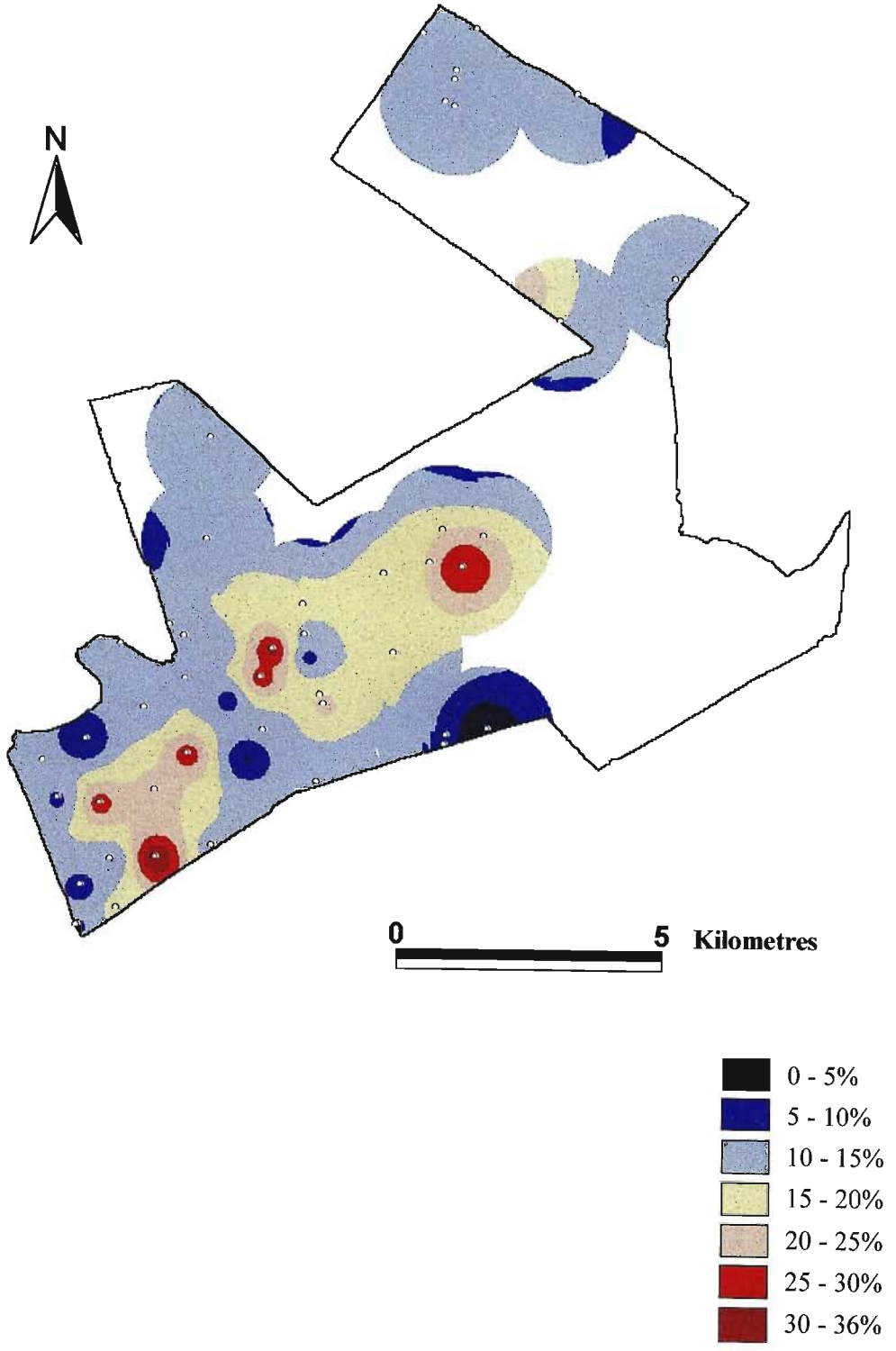
Appendix C. Detail of the number of pitfall traps recovered and those not recovered at each site.

Site number	Number pitfalls recovered	Number pitfalls not recovered	Reason not recovered
1.1	10	0	
1.2	10	0	
1.3	10	0	
1.4	10	0	
1.5	10	0	
1.6	9	1	Pitfall broken
1.7	10	0	
1.8	10	0	
1.9	10	0	
2.1	10	0	
2.2	10	0	
2.3	10	0	
2.4	10	0	
2.5	9	1	Pitfall broken
2.6	10	0	
2.7	10	0	
2.8	10	0	
2.9	10	0	
3.1	8	2	Flooding
3.2	10	0	
3.3	0	10	Removed by baboons
3.4	9	1	Pitfall broken
3.5	10	0	
3.6	10	0	
3.7	10	0	
3.8	10	0	
3.9	10	0	
4.1	10	0	
4.2	10	0	
4.3	10	0	
4.4	10	0	
4.5	9	1	Pitfall broken
4.6	10	0	
4.7	10	0	
4.8	10	0	
4.9	10	0	
5.1	10	0	
5.2	10	0	
5.3	10	0	
5.4	4	6	Flooding
5.5	9	1	Flooding
5.6	10	0	
5.7	10	0	
5.8	10	0	
5.9	10	0	

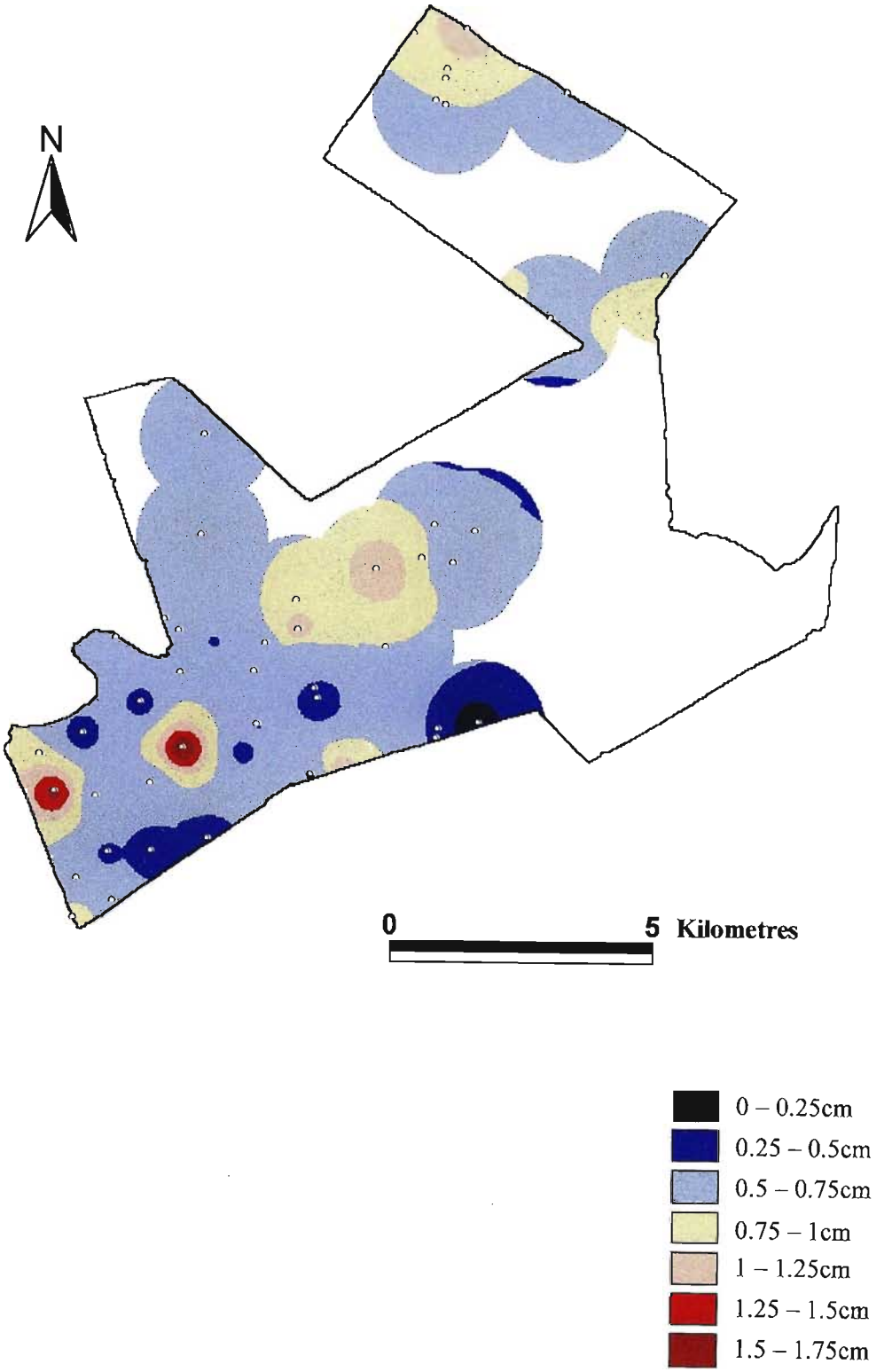
Appendix D. The 1.25km buffer of the invertebrate sample sites. Shaded areas represent the areas included in the analysis, while the white areas were excluded. The white dots are the position of the sample sites.



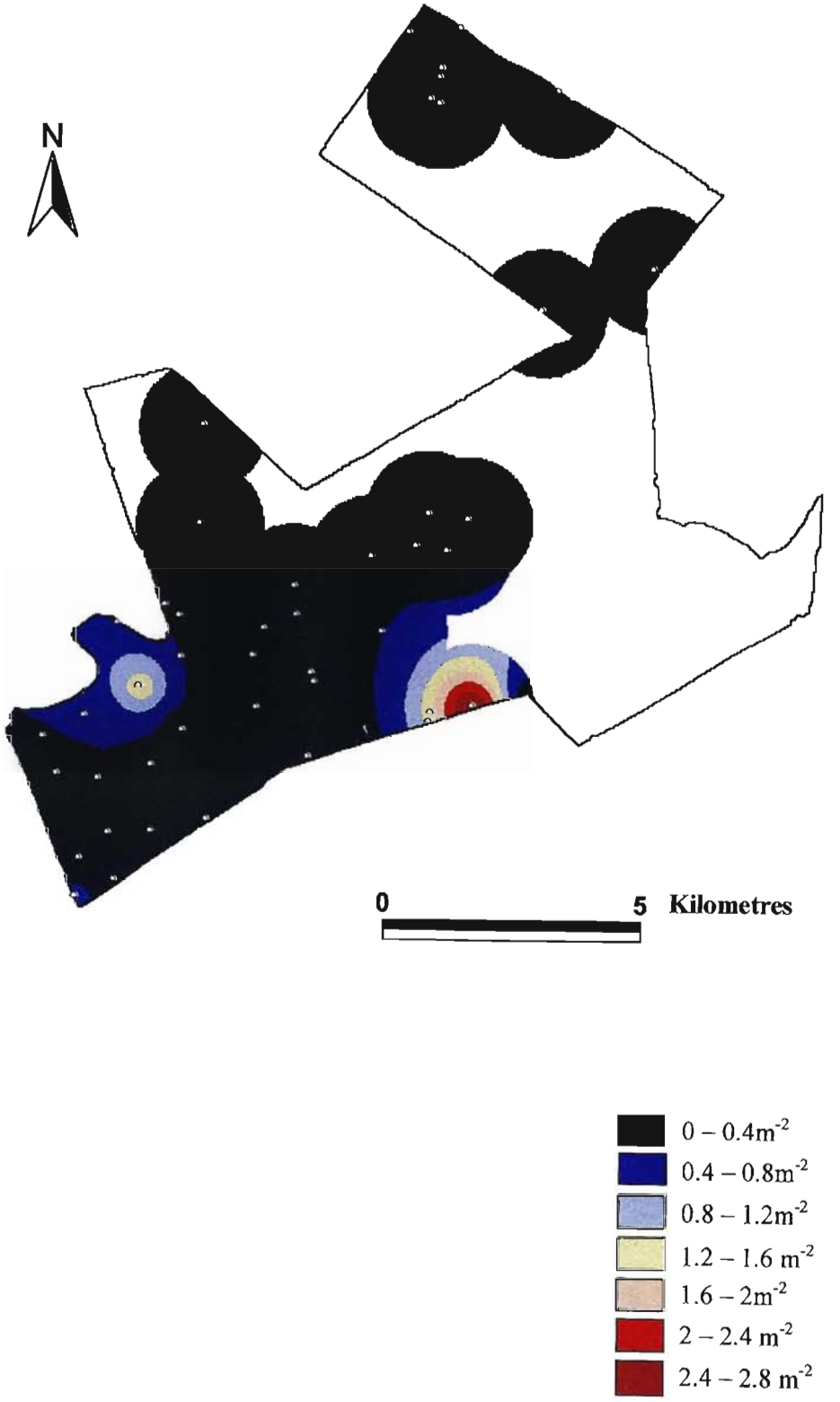
Appendix E. Percentage leaf litter cover for the Greater Makalali Conservancy. Values are an interpolation using GIS from data recorded in quadrats at the 45 sample sites (white dots). Areas further than 1.25km from any sample site were excluded (white area) (see text for explanation).



Appendix F. Average leaf litter thickness for the Greater Makalali Conservancy. Values are an interpolation using GIS from data recorded in quadrats at the 45 sample sites (white dots). Areas further than 1.25km from any sample site were excluded (white area) (see text for explanation).



Appendix G. Vegetation density of woody plants less than 1m tall for the Greater Makalali Conservancy. Values are an interpolation using GIS from data recorded using PCQ density measures at the 45 sample sites (white dots). Areas further than 1.25km from any sample site were excluded (white area) (see text for explanation).



Appendix H. Average rock size for the Greater Makalali Conservancy. Values are an interpolation using GIS from data recorded in quadrats at the 45 sample sites (white dots). Areas further than 1.25km from any sample site were excluded (white area) (see text for explanation).