

**INVERTEBRATE DIVERSITY IN AFROTEMPERATE
FORESTS: SPATIAL AND SEASONAL CHANGES AND
IMPLICATIONS FOR CONSERVATION**

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ABSTRACT

Forests in the Drakensberg Mountains, although generally small and fragmented, represent a wealth of globally significant biodiversity. This is especially true of the invertebrate fauna, which includes a range of localized endemic species. Ground dwelling, flightless invertebrates living in forests show relative immobility and poor dispersal abilities compared to birds, butterflies and other animal taxa. The naturally fragmented state of Afrotropical forests also geographically isolates these taxa. No quantified, systematic surveys of flightless invertebrates have been conducted in Afrotropical forests in the Drakensberg Mountains. This means that, to date, invertebrates have not been considered in the management of these habitats. However, invertebrates are vitally important in ecosystem functioning and maintenance and must be included in management plans.

This study quantified flightless invertebrate diversity in Afrotropical forest patches in the Drakensberg by investigating spatial patterns and seasonal changes in invertebrate diversity. The broad objectives were to:

- 1) Determine the appropriate spatial scale at which conservation of flightless invertebrates should be implemented;
- 2) Determine which season, taxa and sampling methods are most suitable for biodiversity assessment and monitoring in Afrotropical forest; and
- 3) Investigate methods of prioritizing Afrotropical forests for conservation of flightless invertebrate diversity.

Seventeen forest patches in six valleys in four Drakensberg reserves (Rugged Glen Nature Reserve, Royal Natal National Park, Cathedral Peak and Injisuthi) were sampled in the summer of 2004/2005. In addition, three forests at Injisuthi were sampled in March, June, September and December 2004 to enable seasonal comparisons. Sampling methods included soil samples, leaf litter samples, pitfall traps, active search quadrats and tree beats. The study focused on terrestrial molluscs (Class Gastropoda), earthworms (Class Annelida), onychophorans (Class Onychophora), centipedes (Class Chilopoda), millipedes (Class Diplopoda) and ants (Class Insecta). Target taxa were sorted to morphospecies and then identified to species by taxonomic experts.

Seventy-two species and a total of 5261 individual specimens from the six target taxa were collected. Species composition of sites varied along the north-south gradient, and species turnover (beta diversity) was related to the distance between sites. Flightless invertebrate species richness and community structure fluctuated seasonally. Therefore, I recommend that sampling should take place during the wet season (summer months). Molluscs were the most suitable taxon among those surveyed to represent flightless invertebrate diversity and leaf litter samples and active search quadrats are the most suitable sampling methods for flightless invertebrates in forest.

This study compared approaches to prioritizing Afrotropical forests in terms of their invertebrate diversity using ranked species richness with complementarity indices of species presence/absence, taxonomic distinctness (orders, families and genera) and endemism. There was no consistent spatial trend in the priority ranking of forests based on species richness. Complementarity based on species richness only required eight out of 17 forests to represent all 62 species. Although complementarity based on taxonomic distinctness and endemism required fewer sites, not all species were represented. The minimum set of sites identified using complementarity based on species richness and augmented with information on taxa of conservation importance (local endemic and threatened species) was the most rigorous approach to prioritizing Afrotropical forest patches in the Drakensberg for flightless invertebrate conservation.

Urgent conservation interventions are required because invertebrates play a critical role in ecosystem functioning. As many forest patches and invertebrate populations as possible should be protected to conserve the full complement of invertebrate species of the region. Special management attention should be paid to the eight forests identified as priority sites in the complementarity analyses.

Forest patches cannot survive in isolation, so it is important to manage the grassland, riverine vegetation, forest ecotone and forests holistically. Provisional targets were set for the conservation of flightless invertebrates, based on estimates of the requirements for persistence of invertebrates in Afrotropical forest, made within the constraints of available information and expert opinion.

PREFACE

This study was conducted at Rugged Glen Nature Reserve, Royal Natal National Park, Cathedral Peak and Injisuthi in the uKhahlamba-Drakensberg Park, and the dissertation was written in the School of Biological and Conservation Sciences, University of KwaZulu-Natal, Pietermaritzburg, from January 2004 to October 2006 under the supervision of Professor Michelle Hamer and co-supervision of Professor Robert Slotow.

This study represents original work by the author and has not otherwise been submitted in any form for any degree or diploma to any University. Where use has been made of the work of others it is duly acknowledged in the text. The journal "Biological Conservation" was used as a template for formatting and referencing, and hence expressions of Latin origin such as "et al." and "a priori" are not in italics. All tables and figures have been placed in the text in the relevant positions.



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1 INTRODUCTION AND BACKGROUND

1.1 Spatial patterns of diversity

Biodiversity varies in space and time (Rosenzweig, 1995). Well-known spatial patterns of diversity include species-area curves (you will find more species if you sample a larger area), latitudinal gradients (the number of species decreases as you move away from the Equator, north or south), habitat variety (the greater the habitat variety, the greater the species richness), and disturbance (diversity peaks over intermediate disturbance levels) (Rosenzweig, 1995). These spatial patterns of diversity change over multiple spatial scales and local community patterns may be very different from landscape or regional patterns (Crist et al., 2003). However, local patterns are seldom independent of regional patterns of diversity. Species richness patterns are also driven by extinction and colonization processes, of which area and isolation are the main correlates (Watling and Donnelly, 2006). Consequently, spatial patterns of diversity are important for systematic conservation planning because the scale at which information is collected determines the scale at which conservation decisions can be made and management questions answered (Rouget, 2003).

1.2 Systematic conservation planning

Systematic conservation planning is aimed at the representation of a fixed proportion of species or area in a protected or conserved area network (Kerley et al., 2003) and makes use of knowledge of natural ecosystems and an understanding of human impacts on these ecosystems to address conservation issues (Lambeck and Hobbs, 2002). As such, systematic conservation planning is a means of identifying spatially explicit options and priority areas for the conservation of biodiversity (Driver et al., 2003a). Systematic approaches to conservation planning are based on three principles:

- 1) The need to conserve a representative sample of biodiversity, such as species and habitats (the principle of representation);
- 2) The need to conserve the ecological and evolutionary processes that allow biodiversity to persist over time (the principle of persistence); and
- 3) The need to set quantitative biodiversity targets that indicate how much of each biodiversity feature should be conserved to maintain functioning landscapes (Margules and Pressey, 2000; Driver et al., 2003b; Driver et al., 2005).

Margules and Pressey (2000) outlined six stages to achieve these principles:

- 1) Compile data on the biodiversity of the planning region,
- 2) Identify conservation goals for the planning region,
- 3) Review existing conservation areas,
- 4) Select additional conservation areas,
- 5) Implement conservation actions, and

6) Maintain required values of conservation actions.

A similar seven step conservation planning framework, developed by The Nature Conservancy, has been tested and used in the implementation of over 45 regional conservation plans in the United States, Latin America, the Caribbean, Micronesia and Yunnan, China (Groves et al., 2002).

South Africa has a long history of systematic conservation planning. More than thirty systematic conservation planning initiatives have taken place in South Africa over the last two decades (Jack, 2004). Large-scale, regional systematic conservation planning project examples include CAPE, the Cape Action Plan for the Environment (Gelderblom et al., 2003; Younge and Fowkes, 2003); STEP, the Subtropical Thicket Ecosystem Planning project (Cowling et al., 2003) and SKEP, the Succulent Karoo Ecosystem Plan (Driver et al., 2003b). South Africa also has numerous examples of smaller scale conservation planning projects, such as the KwaZulu-Natal Provincial Conservation Plan, Agulhas Plain Conservation Plan, Cape Lowlands Renosterveld Conservation Plan, Greater Addo Elephant National Park Conservation Plan (GAENP), and the Nelson Mandela Metropolitan Open Space System (NM MOSS) (Driver et al., 2003a). CAPE is one of the most detailed and explicit conservation plans to date in the developing world (Balmford, 2003) and highlights how South African research has taken the lead on systematic conservation planning.

Systematic conservation plans for the forest biome in South Africa use guidelines developed internationally, where appropriate. Europe has provided few useful guidelines for conservation planning in the forest biome in South Africa because the European focus has been on consumptive use of forests (Berliner and Benn, 2003). The Australian approach to reserve selection provided useful guidelines for the identification of a reserve system for natural forests in South Africa (Berliner and Benn, 2003) and a systematic conservation plan for the forest biome in South Africa has been developed (Berliner, 2005). Forest has also been incorporated as a broad habitat unit in successful conservation planning exercises such as CAPE (Pressey et al., 2003) and STEP, where targets were set at representation of 100% of the four forest types (Cowling et al., 2003). The KwaZulu-Natal provincial conservation plan of 2002 (Driver et al., 2003a) also includes forest and identifies Montane *Podocarpus* Forest (which includes Drakensberg Montane Forest and Northern KwaZulu-Natal Mistbelt Forest identified by von Maltitz et al., 2003) as a provincial conservation target.

There have been some recent attempts to incorporate invertebrate taxa in conservation planning. For example SKEP used termites, bees and scorpions for expert mapping during the planning stages, the KwaZulu-Natal provincial conservation plan uses invertebrates such as millipedes and Eeley et al. (2001) used butterflies to prioritize forests for conservation in KwaZulu-Natal. However, as yet, few local conservation plans have incorporated flightless or more cryptic invertebrate taxa and several of the most influential South African systematic conservation planning projects, such as CAPE and STEP, did not

include any invertebrate taxa because of insufficient suitable locality data sets. Consequently, large gaps in the conservation of invertebrate populations in South Africa remain, even in formally protected areas. Ways of including invertebrates in conservation planning projects and management activities therefore need to be investigated.

1.3 The importance of invertebrates

Invertebrates may comprise up to 95% of diversity on Earth (Myers et al., 2000). There are currently 77 500 described species of invertebrates in South Africa, accounting for 5.5% of the Earth's invertebrate species (Rouget et al., 2004). Approximately 70% of South African invertebrates are endemic to the South African region (Hamer, 2002). By comparison, there are only 227 mammal species (36 endemics) and 718 bird species (41 endemics) in the country (Rouget et al., 2004). Since invertebrates comprise such a large proportion of the Earth's diversity, they are important in global and regional conservation planning. Any conservation plan that aims to represent biodiversity should include invertebrates.

Invertebrates are also critically important in ecosystem functioning and therefore in the persistence of habitats or ecosystems that we aim to conserve. Invertebrates provide a wealth of ecosystem services, including the regulation of soil fertility, plant pollination, pest control, clean water, and food for animals. Invertebrates also play a regulatory role in decomposition, especially in forest ecosystems (Crossley, 1977). In particular, earthworms and ants accelerate decomposition and increase nutrient availability (Kellert, 1993). Terrestrial molluscs (snails and slugs) also produce soil, concentrate calcium and provide food for vertebrates (Tattersfield et al., 1998). Therefore, direct negative impacts on invertebrate diversity affect the ecosystem as a whole. Without the ecosystem services provided by invertebrates, biomes such as forest would not exist.

For many groups of invertebrates only a small proportion (probably 10%) of species have been described (New, 1993; Samways, 1993). Of those invertebrates that have been named, many are difficult to identify and most cannot be identified unless in the hand (Ward and Larivière, 2004). This taxonomic impediment may be overcome in rapid assessments of biodiversity by using morphospecies, i.e. recognizable taxonomic units (RTUs) that act as surrogates for a wider range of species (Oliver and Beattie, 1996a). Morphospecies analyses focus specialist time and input on critical phases of the research process, thereby improving the time- and cost-efficiency of biodiversity surveys (Oliver and Beattie, 1996b). However, in the absence of taxonomic verification of morphospecies by taxonomic experts, morphospecies may be worthless for biodiversity inventories and area selection in conservation evaluation and biogeographical studies; and they provide only uncertain data for studies on species turnover (Krell, 2004).

In addition to the taxonomic impediment, there is a lack of knowledge on the global and national rates of invertebrate species loss and the reasons for it (Pullin, 1997). Given the

enormous diversity of invertebrates, quantifying threats to individual species is difficult and seldom attempted. Many invertebrates may be more threatened with extinction than plants and vertebrates because most invertebrate species have narrow distributions (Kremen et al., 1993). Lack of information on the diversity, functional niches and life history traits of invertebrates also obstruct invertebrate conservation. Including invertebrates in ecological or conservation studies without such information is problematic.

A common solution to the lack of spatial data for invertebrates is to use taxa for which we do have distributional information as surrogates for spatial pattern in biodiversity as a whole. The use of surrogates is often critical for conservation planning (Margules and Pressey, 2000; Ferrier, 2002; Warman et al., 2004), but not without several potential problems (Ferrier, 2002). The first problem involves the level of congruence between distributional patterns of biodiversity. Despite extensive work on this problem (e.g. Lombard, 1995; Lawton et al, 1998; Howard et al, 1998; van Jaarsveld et al., 1998; Kotze and Samways, 1999; Kati et al., 2004), no definitive solutions have emerged. Cross taxon congruency varies greatly depending on the taxa investigated, the biogeographic history of the region under study, and the spatial scale of analysis (Ferrier, 2002; Bilton et al., 2006). Bias in the geographic coverage of available data is another problem associated with the use of species as surrogates in conservation planning (Ferrier, 2002; Hamer and Slotow, 2002).

Terrestrial invertebrates are also potentially suitable candidates to be ecological indicators (McGeoch, 1998; Andersen, 2004) and have been widely accepted as such (Andersen and Majer, 2004). Invertebrates can be used to show the impacts of environmental stressors on biotic communities because of the significant role that they play in ecosystem functioning. Invertebrate populations are expected to respond to environmental disturbances faster than trees or large vertebrates because of their high rates of population increase, short generation times and comparatively high habitat specificity (Kremen et al., 1993; Oliver and Beattie, 1996a). Consequently, there is a recent trend to use invertebrates, especially insects, rather than vertebrates as indicator taxa (Samways, 1990; Kotze and Samways, 1999). Dragonflies, ground beetles, tiger beetles, moths, butterflies, sawflies and ants have been used as bioindicators in a variety of habitats (McGeoch, 1998). Butterflies in particular have been recommended as indicators of ecosystem integrity (Kremen et al., 1993; New et al., 1995).

1.4 Afrotropical forests

Forest occupies approximately 42 million square kilometres or 32% of dry land globally, of which 17% is found on the African continent (Dajoz, 2000). Forest is the smallest biome in southern Africa (Rutherford and Westfall, 1997; Eeley et al., 2001), covering less than one percent of the combined land area of South Africa, Lesotho and Swaziland (Midgley et al., 1997; Rutherford, 1997; Rouget et al., 2004). Forests in South Africa cover approximately

4867 km² and have a naturally fragmented distribution, with over 20 000 patches ranging in size from <1 ha to >2000 ha, most (71%) of which are <10 ha (Berliner, 2005).

Based on a biogeographic-floristic classification of the South African indigenous forests, there are seven forest groups, subdivided into 25 forest types (von Maltitz et al., 2003). One of the seven forest groups, Northern Afrotemperate Forest shares affinities with Afromontane forests throughout sub-Saharan Africa, which occur as a series of isolated patches comprising the Afromontane archipelago-like regional center of endemism (White, 1983). Nevertheless, South African forests are classified as Afrotemperate, and not Afrotropical, because of their climate (Berliner, 2005).

The Northern Afrotemperate Forest Group consists of five forest types: Marakele Afromontane Forests, Northern Highveld Forests, Northern Highveld Kloof Forests, Drakensberg Montane Forests, and Northern KwaZulu-Natal Mistbelt Forests. Drakensberg Montane and Northern KwaZulu-Natal Mistbelt Forests occur in the Maloti-Drakensberg Bioregion (von Maltitz et al., 2003; Sipkes, 2005). This study focuses on Drakensberg Montane Forest.

Drakensberg Montane Forest occurs at altitudes between 1200 and 2000 m a.s.l., with 73% confined to 1400-1900 m a.s.l. (Killick, 1990; von Maltitz et al., 2003; van de Gevel, 2005). Drakensberg Montane Forest covers a total area of 4863 ha, all of which is found within the Maloti-Drakensberg Bioregion (Berliner, 2005). Forest patches in the bioregion range from less than one hectare to over ten hectares in extent (Hill, 1996), with only three patches over 100 ha (Sipkes, 2005; van de Gevel, 2005). Forest patches are also larger and more numerous in the northern than in the southern Drakensberg because the northern Drakensberg is warmer and wetter (Hilliard and Burt, 1987; von Maltitz et al., 2003).

Most woody communities in the Drakensberg Mountains are restricted to refuge habitats, such as moist, south-facing slopes that are protected from wind and fire (Killick, 1990; von Maltitz et al., 2003). These forests are frost tolerant, but occasional disturbance occurs in the form of heavy snowfalls. Rock falls, landslides and spot-fires (due to natural causes, arson and poor management of surrounding grasslands) also sometimes clear large areas in forests (von Maltitz et al., 2003).

Drakensberg Montane Forest is relatively low in stature (7-10 m) and species-poor compared to the flora of other South African forests (van de Gevel, 2005). *Podocarpus latifolius* (Real Yellowwood) and a mixture of other tree species, including *Olinia emarginata* (Mountain Hard Pear) and *Scolopia mundii* (Red Pear) dominate the canopy (Pooley, 2003; von Maltitz et al., 2003).

The Drakensberg mountain range forms part of the eastern escarpment of the interior plateau of southern Africa. The range runs in a predominantly north-south direction, 150 to 280 km from the coast and from 28.2°S to 31.4°S and 27.1°E to 30.0°E (Eeley et al., 1999; Porter, 1999; Sipkes, 2005). Mean annual precipitation in the Drakensberg ranges from 1000

to 1800 mm and summer (November to March) precipitation accounts for 70% of the total annual precipitation, with rainfall peaking in January (Schulze, 1997). Frost is common from April to September and there are on average eight snowfalls per year, concentrated in July. Mean annual temperature in the Drakensberg is 16°C while the average daily minimum winter temperature is -1.1°C (Schulze, 1997). South-facing slopes are generally cooler and moister than north-facing slopes.

The Drakensberg has one of the longest and strongest conservation histories in southern Africa, with a century of formal protection in certain areas. Parts of the Drakensberg have been declared a World Heritage Site: the uKhahlamba-Drakensberg Park World Heritage Site (UDP). The UDP falls within the Maloti-Drakensberg Bioregion, which includes areas allocated to tourism, private farmlands, timber plantations, communal lands, conservancies and protected areas. The UDP is the largest core protected area within the Maloti-Drakensberg Transfrontier Project (MDTP) planning domain (Figure 1.1). The MDTP is a collaborative initiative between South Africa and the Kingdom of Lesotho that aims primarily to protect the exceptional biodiversity of the Drakensberg and Maloti mountains through conservation, sustainable resource use, and land-use and development planning.

The remote location and difficulty of access spared many of the natural forests in the Drakensberg from the high level of exploitation that other forests in KwaZulu-Natal have historically suffered (Porter, 1999). However, logging did take place in the Drakensberg forests, as is evident from the saw pits at Monks Cowl and Cathedral Peak (Killick, 1990) and the lack of very large, old yellowwood trees in many of the accessible forests. Drakensberg Montane Forest is one of the rarest forest types in South Africa and is classified as Near Threatened based on suggested IUCN endangerment categories for forest types (Berliner, 2005).

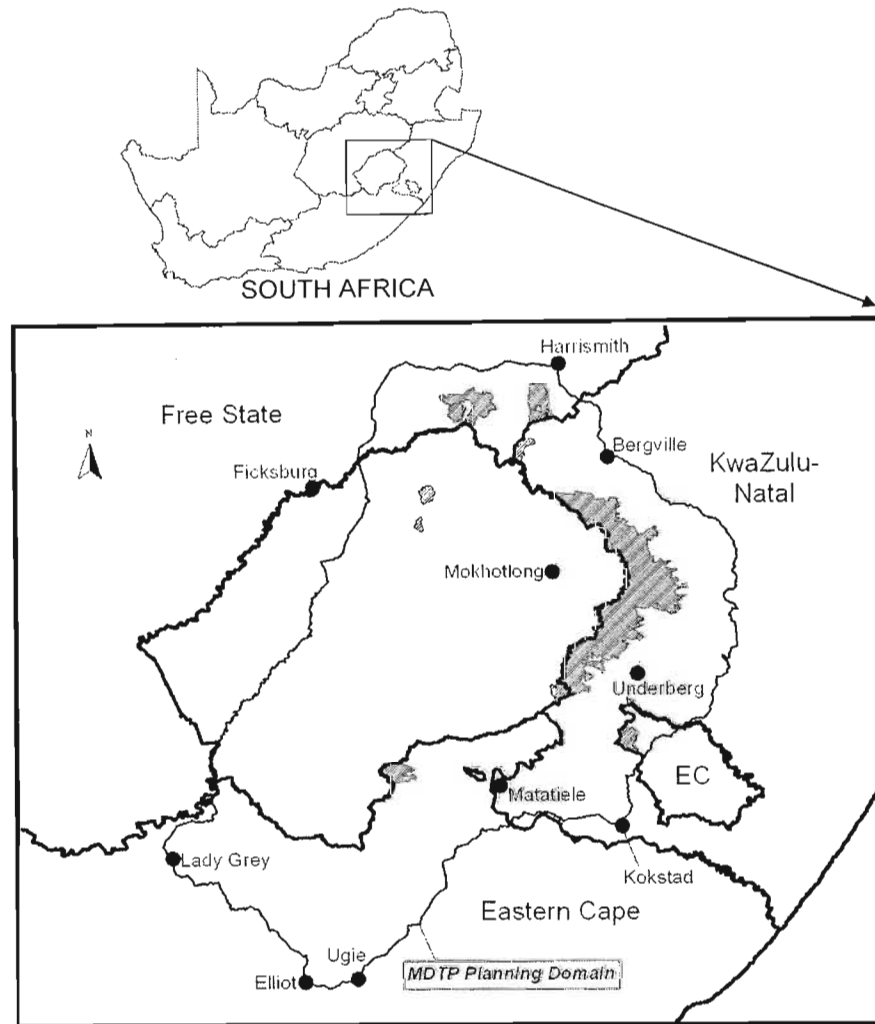


Figure 1.1. Location map of the Maloti-Drakensberg Transfrontier Project (MDTP) planning domain. Protected areas are highlighted in grey.

1.5 Conservation Planning in Afrotropical forests

The fragmented state of Afrotropical forest is problematic for conservation planning. Existing protected areas in KwaZulu-Natal represent 97% of the forest-dependent and forest-associated species of butterflies, birds and mammals (Eeley et al., 2001). Since the resources available for conservation are limited, the goal of conservation planning in Afrotropical forests becomes one of identifying a core network of priority areas within the current reserve network (Eeley et al., 2001).

Forests in the Drakensberg Mountains, although generally small and fragmented, represent a wealth of globally significant biodiversity (Berliner, 2005). This is especially true of the invertebrate fauna, which includes many endemic species (Appendix 1a; Porter, 1999; Derwent et al., 2001). However, this fauna has yet to be fully explored. The complex interactions between climate, geology, geomorphology and fire that led to the fragmented nature of forest patches in the Drakensberg make these patches suitable for the study of

invertebrate species diversity patterns. A better understanding of the invertebrate diversity is required before measures can be considered to address a range of threats to invertebrates, including habitat loss and disturbance. Based on scattered records, species descriptions for individual taxa and expert opinions, at least six invertebrate phyla, thousands of families and tens of thousands of species are likely to occur within the Maloti-Drakensberg Bioregion.

1.6 Invertebrate diversity in Afrotropical forests: spatial and seasonal changes and implications for conservation.

Spatial patterns of diversity are likely to occur at a different scale among less mobile, ground dwelling invertebrates compared to other taxa (Ferrier et al., 1999). In forested north-east New South Wales, Ferrier et al. (1999) found that species turnover for plants, reptiles and birds is associated with variation in environmental variables, whereas patterns of species turnover for ground dwelling spiders, ants, carabid and scarab beetles are more complex and related to both environmental variables and geographic separation of sites. Greater knowledge of the scale of diversity may change the perception of forest endemism and could potentially increase the conservation value of Afrotropical forests in South Africa. With an increased understanding of the conservation value of these forests, conservation management would be better placed to influence actions in terms of protection of forests from fire, alien invasive plants, over-harvesting, erosion caused by hiking trails, and ecotourism development.

The effect of season on invertebrate species richness and community composition needs to be understood to allow assessment of changes in the environment over time. The time of year in which biodiversity surveys take place should be considered (Curry, 1994) and it is important to establish whether data collected in different seasons can be used in comparisons of invertebrate diversity.

Conservation decision-makers need to know whether the forests to be protected can be selected at random, whether certain forests should have priority over others, or whether all forest patches in the region need to be managed and conserved to meet biodiversity targets and conservation goals. There are numerous approaches to prioritizing sites for conservation effort (e.g. Turpie, 1995; Lombard et al., 1997; Margules et al., 2002; Sarkar et al., 2004) and it is unknown whether the approach adopted would influence the results for the prioritization of Afrotropical forest patches in the Drakensberg Mountains for the conservation of flightless invertebrate communities.

1.7 Broad aims and objectives

This study focused on ground dwelling invertebrates with limited mobility (i.e. flightless taxa). Target taxa included terrestrial molluscs (snails and slugs), earthworms, onychophorans

(velvet worms), centipedes, millipedes and ants (wingless workers only), representing a range of functional guilds and life histories.

The overall aim of this study was to quantify flightless invertebrate diversity in Afrotropical forest patches in the KwaZulu-Natal Drakensberg and investigate spatial and seasonal changes in invertebrate diversity and their implications for conservation. The broad objectives were:

- 1) To determine the appropriate spatial scale at which conservation of flightless invertebrate taxa should be implemented and management decisions made in the KwaZulu-Natal Drakensberg. This included three subsidiary goals. First, to quantify flightless invertebrate species turnover at different spatial scales (i.e. forests separated by increasing distance). Second, to determine whether target taxa show similar patterns of species turnover with spatial scale, which would be expected if they are equally affected by habitat isolation, and provided that isolation is a dominant influence on taxon turnover. Third, to investigate environmental and disturbance factors that may influence invertebrate community structure.
- 2) To investigate the natural seasonal changes in species richness and assemblage composition of flightless invertebrates in Afrotropical forest in the KwaZulu-Natal Drakensberg. These data would enable recommendations to be made on which season, taxa and sampling methods are most suitable for biodiversity assessment and monitoring for the conservation of flightless invertebrates in Afrotropical forest.
- 3) To investigate methods of prioritizing Afrotropical forests based on flightless invertebrate diversity, to evaluate the impact of different methods on priority areas identified.
- 4) To bring the findings of this study together to discuss their implications to conservation management, to propose future research, and make recommendations on setting targets for invertebrate conservation in Afrotropical forest, especially in the Drakensberg Mountains.

1.8 REFERENCES

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Appendix 1a. *Known invertebrate species richness and numbers of Drakensberg and southern African endemics (adapted from Porter, 1999). A = Drakensberg invertebrate species richness, B = Invertebrate species endemic to the Drakensberg and C = Drakensberg invertebrate species endemic to South/southern Africa. Molluscs were not included in Porter's (1999) data.*

Phylum	Subphylum	Order	Family	Common Name	A	B	C
Annelida		Oligochaeta	+	Earthworms	3	1	1
Onychophora		Onychophora	+	Velvet worms	2	0	2
Arthropoda	Myriapoda	Diplopoda	+	Millipedes	33	21	21
Arthropoda	Myriapoda	Chilopoda	+	Centipedes	14	1	1
Arthropoda	Hexapoda	Odonata	+	Dragonflies & Damselflies	44	1	6
Arthropoda	Hexapoda	Lepidoptera	+	Butterflies & Moths	74	?	4
Arthropoda	Hexapoda	Coleoptera	Cetoniidae	Fruit chafers	24	?	?
Arthropoda	Hexapoda	Hemiptera	Delphacidae	Planthoppers	?	4	4
Arthropoda	Hexapoda	Neuroptera	+	Lacewings	10	4	4
Arthropoda	Hexapoda	Diptera	Blepharoceridae	Net-winged midges	4	1	2
Arthropoda	Hexapoda	Diptera	Tipulidae	Crane flies	61	32	32
Arthropoda	Hexapoda	Diptera	Empididae	Dance flies	30	21	30
Arthropoda	Hexapoda	Diptera	Asilidae	Robber flies	33	?	?
Arthropoda	Hexapoda	Diptera	Rhagionidae	Wormlion flies	?	1	1
Arthropoda	Hexapoda	Diptera	Tachinidae	Tachinid flies	?	2	2
Arthropoda	Hexapoda	Mecoptera	Bittacidae	Hanging flies	6	1	1

+ More than one family

? Unknown number

2 TURNOVER IN INVERTEBRATE SPECIES COMPOSITION OVER DIFFERENT SPATIAL SCALES, FROM SITE TO SUB-REGIONAL SCALES IN AFROTEMPERATE FOREST

ABSTRACT

Ground dwelling, flightless invertebrates have poor dispersal abilities. This is an important consideration for their conservation in the Afrotemperate forests of the Drakensberg Mountains in South Africa, where they are geographically isolated by the naturally fragmented state of forests. Here I examine the spatial scale at which conservation and management decisions should be made for flightless invertebrates. Seventeen Afrotemperate forests in four reserves across the Maloti-Drakensberg Bioregion were sampled using soil and leaf litter sampling, pitfall traps, active search quadrats and tree beats. Seventy-two species were recorded, comprising 31 mollusc, nine earthworm, one onychophoran, six centipede, 12 millipede and 13 ant species. Significant positive autocorrelation at distances <1.3 km between sites showed that the species composition of these sites was more similar than expected by chance. Canonical correspondence analysis indicated that latitude (distance); fire history (disturbance) and mean annual precipitation were the most important geographical and environmental factors governing invertebrate assemblage composition in forests in the region. Species turnover between sites significantly contributed to sub-regional invertebrate diversity. Species turnover (measured as β_{sim}) was detected at all spatial scales investigated, namely between forests within valleys, between valleys and across the sub-region sampled. ANOSIM showed that, in general, there was an increase in species turnover with increasing distance between sites. This implies that a number of forests across the Drakensberg would need to be protected to encompass and conserve the high diversity of forest dwelling invertebrates in the region.

2.1 INTRODUCTION

Biodiversity varies in space and time (Rosenzweig, 1995) and species richness patterns are often strongly scale-dependent (Lennon et al., 2001). The rate at which species are accumulated with increasing area (coarsening scale) depends on the location of the area. Spatial scale is therefore important for systematic conservation planning because the scale at which information is collected determines the scale at which conservation decisions can be made and management questions answered (Rouget, 2003). Consequently it is important to measure diversity at the scale of the smallest manageable landscape unit, such as individual forests.

Species diversity has three major components: alpha (α), beta (β) and gamma (γ) diversity (Koleff et al., 2003; Magurran, 2004). Alpha diversity measures local diversity within

a defined assemblage or homogenous habitat (Magurran, 1988; 2004). Beta diversity, or differentiation diversity, is a measure of species turnover between assemblages or across habitats (Magurran, 1988; 2004). It measures the difference (or similarity) in a range of habitats or samples in terms of the variety (and sometimes the abundances) of species found in them (Magurran, 1988). Beta diversity reflects biotic change or species replacement and has been used to explain changes in species composition along environmental gradients, the degree of association or similarity of sites or samples, and the identification of biogeographical boundaries or transition-zone patterns and their implications for conservation planning (Koleff et al., 2003). Magurran (1988; 2004) defines gamma diversity as the next scale of inventory diversity above alpha diversity i.e. the diversity of a larger unit such as an island, landscape or region, and gamma diversity is therefore beyond the scope of this study.

Spatial patterns of species richness and turnover are fundamental for systematic conservation planning and provide insight on the spatial scale at which management decisions for the conservation of biodiversity should be made. Common spatial patterns include the species-area relationship and the latitudinal gradient in species richness (Rosenzweig, 1995). Species richness varies with large-scale processes (such as latitude, longitude and altitude) and small-scale processes (such as competition and predation) (Gaston and Blackburn, 2000). Sites that are close together are more likely to be similar in terms of species richness and assemblage composition than by chance (Legendre and Legendre, 1998; Dale, 1999). Such patterns in species distribution are a result of spatial structuring in the underlying environmental factors that influence the distribution of species.

Ground dwelling invertebrates are expected to show a higher degree of species turnover than vertebrates because they are influenced by both environmental variables and geographic separation of sites (Ferrier et al., 2004). The spatial scale at which this trend is observed is related to biogeographic history and isolation, mobility of taxa, and rates of evolution within taxa. Afrotropical forest patches in the KwaZulu-Natal Drakensberg, South Africa are generally small (<10 ha) and naturally fragmented such that forest-dependent taxa are geographically isolated (Eeley et al., 1999; Eeley et al., 2001). Soil and leaf litter invertebrates generally have poor dispersal abilities (Endrödy-Younga, 1989) and are often restricted to their specific microenvironments. The South African terrestrial mollusc fauna shows high levels of endemism, relictual taxa and explosive radiations in the Charopidae (*Trachycystis*) and Streptaxidae (*Gulella*) (Herbert, 1998) because most terrestrial molluscs have poor active dispersal capabilities (Tattersfield et al., 2001). For these taxa in fragmented environments such as Afrotropical forest patches, species turnover should increase over increasing spatial scale.

Investigation of invertebrate community composition and species turnover among forest sites is warranted because conservation emphasis has been placed on plants and

certain vertebrate groups (Oliver and Beattie, 1993; Pullin, 1997), which may not reflect patterns of invertebrate diversity. Ferrier et al. (1999) found that species turnover in plants, reptiles and birds in forested New South Wales was mainly related to variation in environmental variables, but that ground dwelling arthropods were influenced by both environmental variation and geographical separation of sites ranging from a few hundred meters to over 350 km. Therefore, successful vertebrate and floral conservation does not necessarily ensure adequate conservation of invertebrate populations (New et al., 1995) or reflect invertebrate patterns of diversity.

The inclusion of all invertebrate species in any biodiversity assessment is impractical because of the sheer abundance and diversity of invertebrates and the associated taxonomic impediment (Oliver and Beattie, 1996a). Therefore, a priori targeting a group of relatively well-known taxa (Oliver and Beattie, 1996a; New, 1998) is the logical starting point for investigating species turnover from site to local and sub-regional scales. Target taxa in this study refer to six ground dwelling, flightless invertebrate groups, namely molluscs, earthworms, onychophorans, centipedes, millipedes and ants (workers only). Here I examine the distribution of these target taxa across indigenous forest in the Maloti-Drakensberg Bioregion to:

- 1) Investigate flightless invertebrate species composition among sites and species turnover at different spatial scales (i.e., forests separated by increasing distance) to provide insight into the appropriate scale at which conservation and management decisions should be made for the conservation of flightless invertebrates.
- 2) Determine whether target taxa show similar patterns of species turnover with spatial scale, which would be expected if they are equally affected by habitat isolation, and provided that isolation is the dominant influence on taxon turnover.
- 3) Investigate environmental and disturbance factors that may influence invertebrate community structure.

2.2 MATERIALS AND METHODS

2.2.1 Study sites

Flightless invertebrate diversity was examined in Afrotropical forests in four reserves located in the uKhahlamba-Drakensberg Park World Heritage Site within the Maloti-Drakensberg Bioregion: Rugged Glen Nature Reserve, Royal Natal National Park, Cathedral Peak and Injisuthi (Figure 2.1). In total 17 forest patches were sampled, three at Rugged Glen, eight at Royal Natal, one at Cathedral Peak and five at Injisuthi (see Appendix 2a for detailed site data).

These forests were situated in moist, sheltered areas on south-facing slopes within valley systems, which generally run east to west, perpendicular to the main north-south

mountain escarpment (Figure 2.2). Two valleys were sampled at Royal Natal National Park (Thukela Gorge valley and Devil's Hoek valley) and Injisuthi (Yellowwood Forest valley and van Heyningen's Pass valley) and one each at Rugged Glen Nature Reserve (Forest Walk valley) and Cathedral Peak (Rainbow Gorge valley). Three forests were sampled in Forest Walk valley, four forests each in Devil's Hoek valley and Thukela Gorge valley, one forest in Rainbow Gorge valley (in which four sites were sampled), four forests in van Heyningen's Pass valley and one forest in Yellowwood Forest valley.

2.2.2 *Sampling methods*

Sampling took place during the summer of 2004/2005. For each forest, one site was chosen that was approximately in the centre of the patch and easily accessible. At each site a range of sampling methods, both active and passive, was employed to sample the invertebrate community. One 15 m transect was laid at each site, starting at least five meters away from the path (or forest edge where a path did not cut through the forest). The transect line was positioned at right angles to the path or forest edge.

Soil sampling

Soil sampling was undertaken to collect soil dwelling invertebrates. Six samples were collected from each transect. One 300 ml soil core was taken every 3 m along the transect line, starting from 0 m. Surface leaf litter and vegetation were cleared away and soil samples collected by digging a hole. Soil samples were placed in Berlese funnels for 48 hours to extract invertebrates. After 48 hours the soil in the funnel was checked for large invertebrates unable to crawl through the 1 mm² gauze.

Pitfall traps

Six pitfall traps per transect were set on the forest floor to collect ground dwelling invertebrates. Plastic 125 ml screw top jars (75 mm deep and with an opening 40 mm in diameter) were placed into the holes dug for the soil samples. Jars were half filled with a glycerol-ethanol mixture. Traps were covered with a white, 90 mm diameter plastic lid, held 30 mm above ground level on a wire frame to minimize evaporation in hot weather, reduce flooding

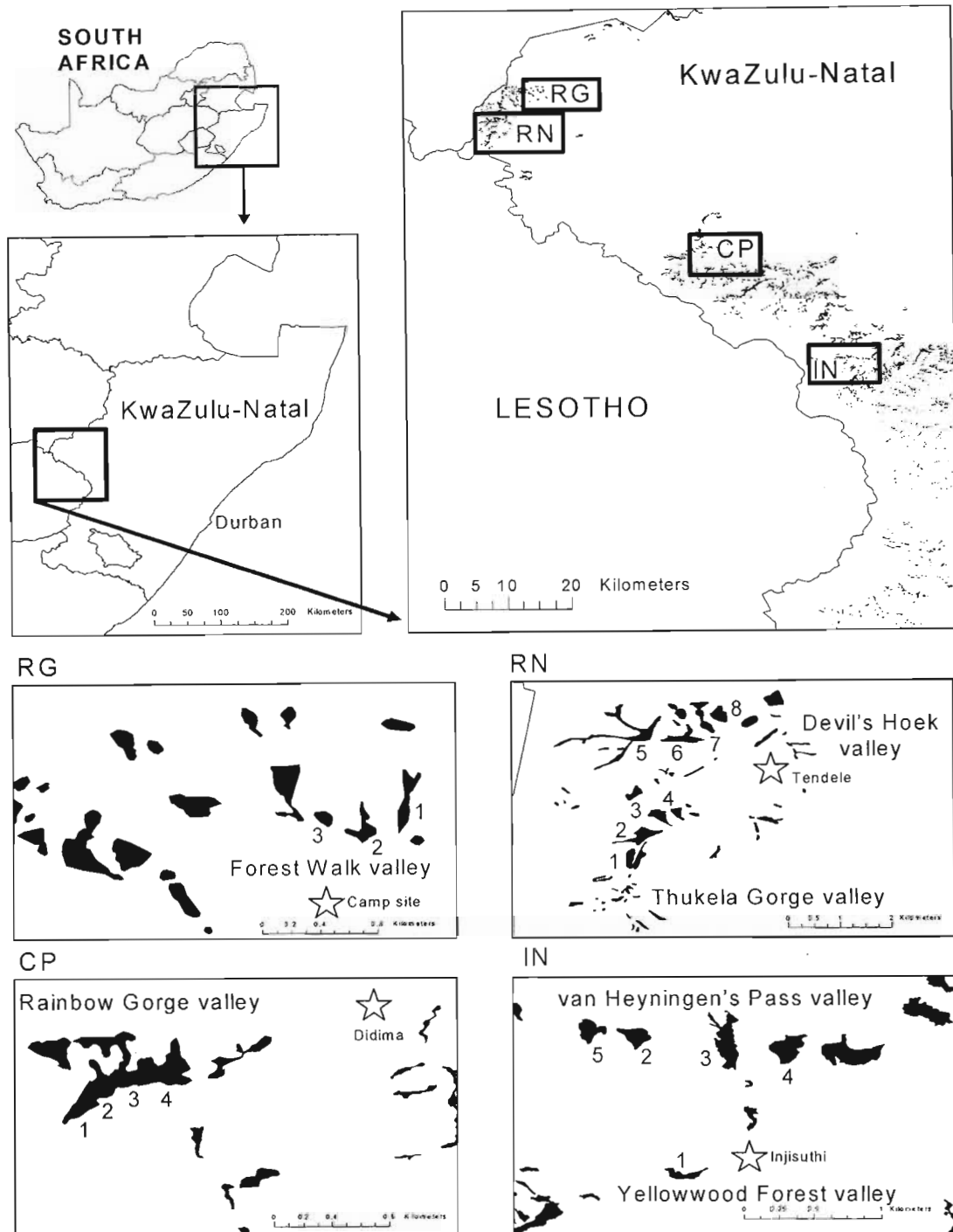


Figure 2.1. Location of study sites in KwaZulu-Natal Province, South Africa (top left). The four reserves within the uKhahlamba-Drakensberg Park are: (RG) Rugged Glen Nature Reserve, (RN) Royal Natal National Park, (CP) Cathedral Peak and (IN) Injisuthi (top right). The study area within each reserve is enlarged (bottom four maps) showing the valleys and forest sites sampled. The numbered forest sites in each reserve (bottom four maps) correspond with the forest sites in Appendix 2a. Afrotemperate forest patches are shown in black and hatted camps and campsites are indicated with a star.

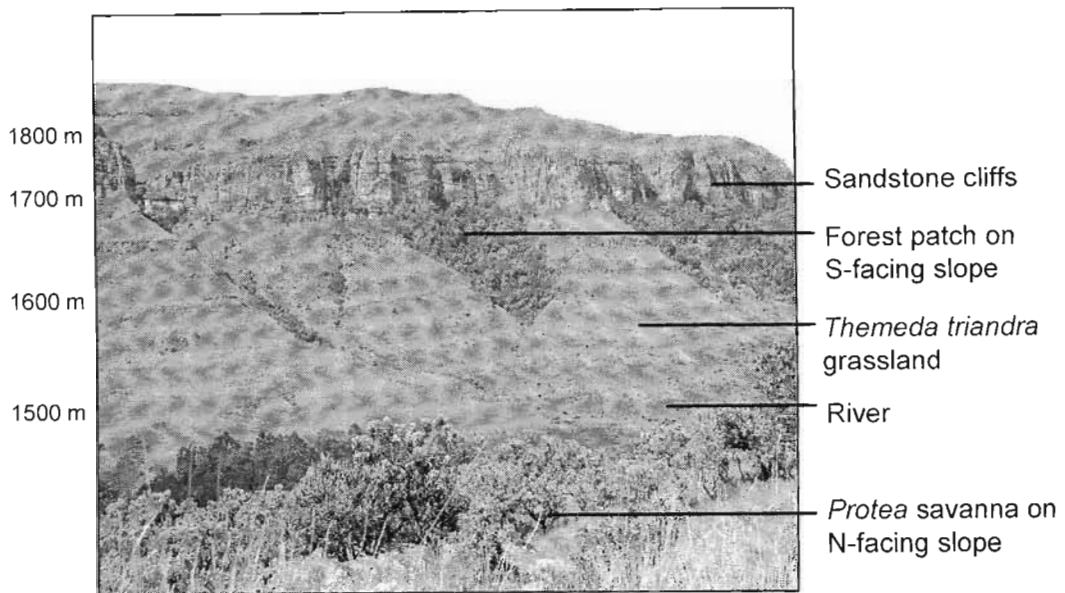


Figure 2.2. Photograph of van Heyningen's Pass valley at Injisuthi illustrating the location of forest patches on the south-facing slope below the sandstone cliffs. The forest in the centre of the photograph is Injisuthi site 4.

within the jar if it rained, and to limit the quantities of leaves and twigs that fell into the jar. Pitfall traps were left in the field for six days to collect invertebrates that were not active when other sampling took place, or that were cryptic or difficult to catch. Invertebrates were separated into target and non-target taxa in the laboratory.

Leaf litter samples

Leaf litter samples were taken to specifically target micro-molluscs. Micro-molluscs are species that as adults have shells smaller than 5 mm maximum diameter (Emberton et al., 1996). Two leaf litter samples were taken, one at 0 m and the other at 15 m along each transect and approximately 1 m to one side of the transect in an area that had not been disturbed by the collectors. Sufficient leaf litter was collected to fill a two litre container for each sample. Both live and dead molluscs were identified. Although leaf litter samples specifically targeted micro-molluscs, other target taxa encountered while searching for micro-molluscs were included in analyses.

Active search quadrats

One set of five contiguous 2 m x 2 m quadrats, covering an area of 20 m², was marked with tape measures and positioned at right angles to a path or forest edge (which ever was closest) on undisturbed ground. Quadrats ran parallel to the transect line but were independent of it. All leaf litter, rocks, logs, vegetation below 0.5 m and the top 50 mm of soil covering the entire area were thoroughly searched for target taxa.

Tree beating

Tree beating was undertaken to collect tree dwelling molluscs and ants. Ten trees were chosen per forest, based on their proximity to the transect, accessibility and availability of a suitable branch to beat. Consequently, only under-storey trees were sampled. One branch of each tree was beaten five times with a wooden stick. A white, flat, round, cotton collecting net of diameter 0.7 m was held just below the branch to collect all molluscs and ants that fell off the branch during beating. Tree species chosen varied according to site (Appendix 2b).

Preparation of individuals

For each 2 m x 2 m quadrat and tree beat, the number of individuals of target taxa was recorded and duplicate specimens and all non-target invertebrates were released. One individual per species per site was collected. Earthworms collected in the soil samples, litter samples and quadrats were prepared as follows: each individual was rinsed in water, preserved in a weak (40%) solution of ethanol, allowed to dry for four minutes and then fixed in 4% formalin. All other invertebrates were frozen and then preserved in 70% ethanol. Other non-target taxa found in the soil samples, pitfall traps and leaf litter samples were retained and preserved for potential future analysis, but not identified or included in this data set.

Target taxa were sorted to morphospecies in the laboratory and identified to species by respective taxonomic experts. Morphospecies were separated using easily recognisable morphological differences (*sensu* Oliver and Beattie, 1996a). Morphospecies were identified by experts as follows: molluscs, Dr Dai Herbert (Natal Museum); earthworms, Dr Danuta Plisko (Natal Museum); onychophorans, centipedes and millipedes, Prof. Michelle Hamer (UKZN); and ants, Dr Hylton Adie. The reference collection is located in the School of Biological and Conservation Sciences, University of KwaZulu-Natal, Pietermaritzburg, South Africa and will be deposited in the Natal Museum, Pietermaritzburg for use in future studies.

Sampling saturation

Sampling intensity was low because of time and cost constraints, and consequently sampling saturation was not fully achieved. Sample-based species-accumulation curves (Gotelli and Colwell, 2001) were plotted for each site using the software package PRIMER (Clarke and Gorley, 2001). Species-accumulation curves were plotted using person hours and not sampling replicates (each tree beat, each soil sample, etc.) so that the five different sampling methods used at each site could be included. Presence/absence data were transformed to reflect the approximate number of person hours taken for field sampling and processing of each replicate of each sampling method. Colwell and Coddington (1994) recommended randomization of the sample order to eliminate the arbitrariness of the order in which samples are added, which affects the shape of species-accumulation curves. Therefore,

species-accumulation curves were plotted with original (unrandomized) data (Appendix 2c) and using 999 permutations to randomize the sampling replicates (Appendix 2d). The original data showed that saturation was not reached for active searching of quadrats or leaf litter sampling, but additional replicates were not collected for these methods because they were the most time consuming and labour intensive sampling methods. Furthermore, randomized species-accumulation curves approached an asymptote for most sites sampled, suggesting that with all techniques combined sampling was close to saturation at most sites. Furthermore, observed species richness of tropical arthropods rarely reaches an asymptote, even with intensive sampling (Gotelli and Colwell, 2001).

To avoid the problems of pseudoreplication (Hurlbert and Hurlbert, 2004) data from the replicates taken at each site (six soil samples, six pitfall traps, two leaf litter samples, five quadrats and ten tree beats) were combined into a single datum per sample method per site. Additional sampling in certain forests was not possible because of the small size of the forest patch and difficulty of finding suitable (i.e. away from the edges of streams, paths and cliffs) and accessible areas within the forest that would provide independent replicates, as well as time and financial constraints. Therefore, a constant sampling effort (i.e., one site per forest, see above sampling methods) was employed in all forests. However, most studies of community ecology standardize sampling effort by area, sampling more sites in larger habitat patches (Gotelli and Colwell, 2001). I have not adopted the usual, standardized sampling approach because of accessibility, time and financial constraints. Instead, the size of the area sampled was kept constant across all forests sampled, regardless of patch size. As a result, species richness values reported here are minimum estimates.

Environmental variables

Environmental variables are summarised in Appendix 2a. Latitude, longitude, altitude and aspect were recorded in the field using a hand-held Garmin GPS and checked against 1:50 000 hiking maps for the uKhahlamba-Drakensberg Park. Mean annual precipitation (MAP) was obtained from Schulze (1997). Forest patch size (area) was calculated in the GIS package ArcMap 8.3. Forests were recorded as burned if they had been burned in the previous two years and still showed signs of burned branches and charcoal in the leaf litter.

2.2.3 Analyses

The results from all sampling methods were combined to calculate the number of species collected for each target taxon at each site (species richness). The four sites in Rainbow Gorge forest at Cathedral Peak were used to establish the accuracy and precision of species richness estimates, because Rainbow Gorge was the only patch in which more than one site was sampled. However, for consistency, only one of the four sites sampled in Rainbow

Gorge forest was used in analyses of species composition and turnover among sites; the site with the highest species richness (site 3) was chosen.

Spatial autocorrelation

Sites that are close together are more likely to be similar in terms of species richness and assemblage composition than by chance (Legendre and Legendre, 1998; Dale, 1999). This lack of independence between pairs of observations at given distances in space is known as spatial autocorrelation and is common in ecological data (Dale, 1999; Diniz-Filho et al., 2003). Spatial autocorrelation in the assemblage composition of forest sites was examined using Mantel test correlograms (Legendre and Legendre, 1998) in PASSAGE (Rosenberg, 2001). A correlogram plots the relationship between separate distance classes (x-axis) and a spatial autocorrelation coefficient (in this case Mantel r values) calculated across pairs of sites within that distance class (y-axis) (Legendre and Legendre, 1998). Mantel tests were used to compare two matrices: a matrix of the Jaccard distance in assemblage composition of sites, calculated from species presence/absence data, and a matrix of the geographical (spherical) distance between sites, measured in kilometers, calculated from longitude and latitude coordinates. The Mantel test investigated the null hypothesis of independence of the elements of the two matrices using a Monte Carlo test (999 permutations). Mantel test correlograms were constructed separately over six, eight and ten distance classes, and in each case distance classes were determined such that there were equal numbers of pairwise comparisons in each class. Mantel test coefficients range from -1 to 1 , with positive coefficients indicating positive spatial autocorrelation, i.e., proximate sites have similar species composition, and negative coefficients indicating negative spatial autocorrelation, i.e., proximate sites have very different species composition (Legendre and Legendre, 1998; Rosenberg, 2001).

Canonical correspondence analysis

The pattern of variation in assemblage composition (for all species combined and for each target taxon separately) across sites and the influence of environmental variables on this variation were examined using canonical correspondence analysis (CCA) in CANOCO 4.5 (Ter Braak and Šmilauer, 1998). In a CCA the ordination axes are constrained to be the best linear fit to the environmental variables provided. These environmental variables were: latitude (used here as a surrogate for distance), altitude, patch area, aspect, mean annual precipitation (MAP), and fire history (see Appendix 2a). A Monte Carlo test (499 permutations) (CANOCO; Ter Braak and Šmilauer, 1998) was used to test whether assemblage composition was significantly influenced by the environmental data. Biplots were drawn to illustrate the relationship between the six environmental variables and ordination site scores for all target taxa combined and separately for each target taxon. On a biplot,

points represent sites and environmental variables are represented by vectors (arrows) showing the direction of maximum variation, with the length of the vector related to the importance of the environmental variable.

Species turnover

There are at least 24 published measures of beta diversity, which can be divided into four main groups: measures of continuity and loss; measures of species richness gradients; measures of continuity; and measures of gain and loss (Koleff et al., 2003). β_{sim} is based on actual compositional differences (species gains and losses) between assemblages and is not influenced by local species richness gradients (Lennon et al., 2001; Koleff et al., 2003). Therefore, β_{sim} is the preferred measure when there are large differences in species richness between sites (Magurran, 2004).

The beta diversity measure, β_{sim} (Lennon et al., 2001), was used to compare species turnover at three spatial scales: between forests within valleys, separately between pairs of valleys, and across all valleys within the study region. To calculate β_{sim} , a (the total number of species common to both sites), b (the number of species present in the neighbouring site but not in the focal site, i.e. species gain) and c (the number of species present in the focal site but not in the neighbouring site, i.e. species loss) were first calculated for each pair of sites. The original β_{sim} equation (Lennon et al., 2001) was re-expressed by Koleff et al. (2003) in terms of these matching/mis-matching components (a , b and c) as:

$$\beta_{sim} = \frac{\min(b, c)}{\min(b, c) + a}$$

Using the smaller value of b or c in the denominator reduces the impact of large differences in species richness (Magurran, 2004). At the first level, within valleys, β_{sim} was first determined between each pair of sites (i.e. between each pair of forests within that valley) and then the mean β_{sim} across these pairs of sites was determined. Likewise, at the next level, across valleys, β_{sim} was first determined between each pair of sites where one site was taken from one valley and the second site from the second valley, and the mean β_{sim} determined across these pairs of sites. Finally, β_{sim} was calculated between pairs of valleys (based on the pooled species presence/absence for each valley) and mean β_{sim} determined across the region.

To further examine turnover in species composition Bray-Curtis dissimilarity matrices were constructed using presence/absence data for all taxa combined and separately for each target taxon across the 17 forests in PRIMER (Clarke and Gorley, 2001). One-way analysis of similarity (ANOSIM) was then performed to test the null hypothesis of no difference in species composition between valleys (Clarke, 1993). ANOSIM is a nonparametric test applied to the rank dissimilarity matrix, using a permutation procedure (999 permutations). ANOSIM calculates the R statistic, which provides a relative measure of separation of a priori

defined groups and ranges from zero (no difference among groups) to one (all samples within groups are more similar to one another than any samples from different groups).

2.3 RESULTS

Seventy-two flightless invertebrate species were recorded (Appendix 2e), comprising 31 mollusc, nine earthworm, one onychophoran, six centipede, 12 millipede and 13 ant species. A total of 5261 individual specimens from the six target taxa were collected (Appendix 2f). The one onychophoran species was excluded from further analyses. Molluscs generally contributed the highest number of species to the total species richness of sites, which was not unexpected since molluscs comprised 31 (43%) of the 72 species recorded. Two species (a centipede, *Rhysida afra afra*, and ant sp. 4) were recorded in all sites sampled. Species richness varied within a forest (the four sites at Cathedral Peak), among forests within the same valley, and among reserves, with a mean of 26.9 ± 6.0 SD species and median species richness of 27.5 species ($n = 20$ sites). Species richness varied from 16 (Royal Natal site 8) to 36 (Injisuthi site 5) species per site. The northern most sites (in Forest Walk Valley at Rugged Glen and Devil's Hoek Valley at Royal Natal) generally showed lower species richness. This was most likely related to the level of disturbance in these northern forests, which showed signs of being burned (e.g. charcoal in the leaf litter, burned logs and branches, and very few shrubs). Species richness of the four sites within one forest patch, Rainbow Gorge forest at Cathedral Peak, had a median species richness of 26.5 species and a range of 22 to 30 species. This suggests that the accuracy and precision of estimates of species richness in other forest patches are fairly reliable.

2.3.1 Spatial autocorrelation

The pattern of spatial autocorrelation was similar irrespective of the number of distance classes across which this was calculated (six, eight or ten) and, for convenience, results across six distance classes only are represented here (Figure 2.3). Significant positive autocorrelation (Mantel $r = 0.477$, $P < 0.001$) was found between sites at distances of < 1.3 km apart, indicating that the species composition of these sites was more similar than expected by chance. In other words, significant positive spatial autocorrelation was present between sites within valleys. Significant negative spatial autocorrelation (Mantel $r = -0.214$, $P = 0.025$) was also found at middle distances, between sites 8 to 27.2 km apart (i.e. between sites at Injisuthi and Cathedral Peak).

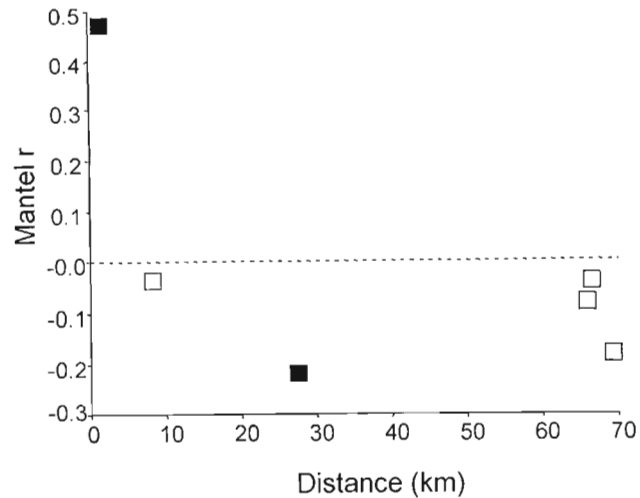


Figure 2.3. Mantel test correlogram showing spatial autocorrelation in assemblage composition between sites across six distance classes (classes determined by equal number of site pair comparisons). Closed symbols represent the distance classes for which the Mantel tests were significant.

2.3.2 Effect of environment on assemblage composition

Invertebrate assemblage composition differed among sites. The CCA of all taxa combined showed a similar pattern to that of an unconstrained correspondence analysis (CA) (i.e., with environmental variables excluded), indicating that no important variables had been overlooked in the CCA. The variance inflation factor was <10 for all six environmental variables, confirming that no multicollinearity was present for the included environmental variables. The first two axes in the CCA accounted for 31.0% and 51.8% of the cumulative percentage variance of the species-environment relationship, respectively. The Monte Carlo test confirmed that both the first axis ($F = 1.985$, $P = 0.002$) and all canonical axes ($F = 1.908$, $P = 0.002$) were highly significant (Figure 2.4) indicating that the six included environmental variables had a direct influence on assemblage composition. Latitude (used here as a surrogate for distance between sites) was strongly related to both the first and the second axis. Sites located within the same valley were generally closely grouped, while sites located furthest apart by distance (latitude), i.e., Rugged Glen and Injisuthi, were represented at opposite ends of the first axis. Axis 1 was also related to fire history and this axis primarily separated unburned sites at Injisuthi, Cathedral Peak and Royal Natal from burned sites at Royal Natal and Rugged Glen. Fire history confounded the latitudinal effect since the burned forest sites, in Forest Walk valley (Rugged Glen) and Devil's Hoek valley (Royal Natal sites 5-8), were also the most northern sites sampled. The second axis was most strongly related to mean annual precipitation (MAP) and aspect, which primarily separated sites at Rugged Glen and Injisuthi from sites at Royal Natal and Cathedral Peak.

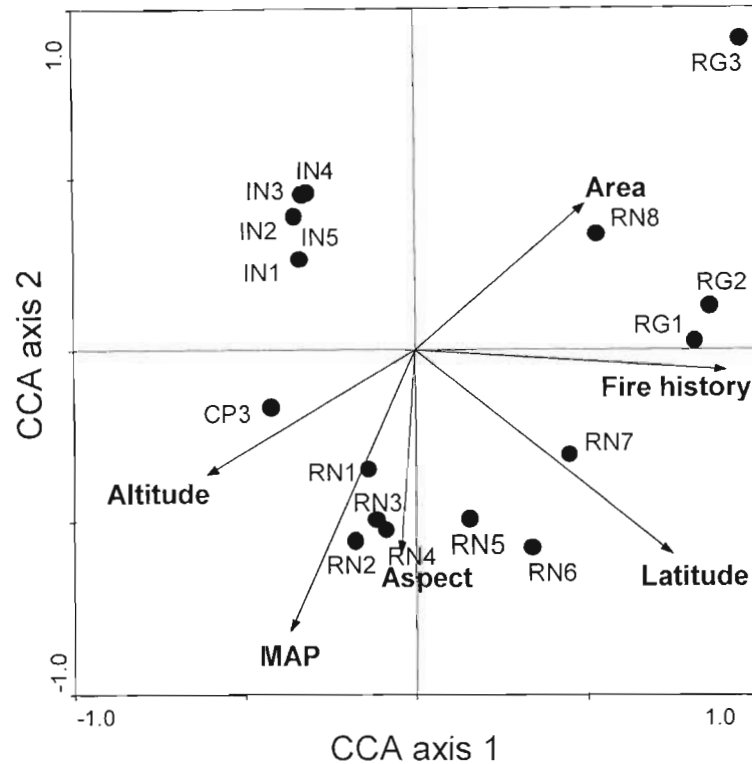


Figure 2.4. Canonical correspondence analysis (CCA) for all target taxa combined, showing sites and environmental variables. The first and second axes account for 51.8% of the cumulative percentage variance of the species-environment relationship. RG = Rugged Glen, RN = Royal Natal, CP = Cathedral Peak and IN = Injisuthi. Site numbers correspond to Appendix 2a. MAP = mean annual precipitation

The variance inflation factors for all six environmental variables were <10 for molluscs and millipedes, showing no multicollinearity of environmental variables. The Monte Carlo tests for molluscs and millipedes confirmed that the first canonical axis (molluscs: $F = 3.079$, $P = 0.002$; millipedes: $F = 3.423$, $P = 0.014$) and all canonical axes (molluscs: $F = 2.402$, $P = 0.002$; millipedes: $F = 2.155$, $P = 0.002$) were significant, indicating that the included environmental variables had a direct influence on assemblage composition in these two taxa. The CCA biplot for molluscs closely resembled the CCA biplot of all taxa combined, which was expected since molluscs comprised 31 (43%) of the 72 species sampled. The Monte Carlo tests for earthworms, centipedes and ants were not significant for either the first or all canonical axes.

2.3.3 Species turnover among sites

Species turnover, measured as β_{sim} , varied within and among the three spatial scales investigated (Table 2.1). Turnover did not increase uniformly with increasing distance between sites either within valleys or between valleys, although turnover was generally

greater between than within valleys, suggesting some distance (isolation) effect. Species turnover appears to reflect a combination of the distance between sites, the site-specific environmental conditions and disturbance history, because within valleys β_{sim} was higher for burned valleys than unburned valleys. Species turnover across the whole region sampled was lower than for most comparisons within or between valleys, possibly because pooled valley data was used.

ANOSIM confirmed that, in general, species turnover increased with increasing distance between sites (Table 2.2). For small distances between pairs of valleys, species turnover for all target taxa combined was generally non-significant, whereas for large distances between pairs of valleys, species turnover was generally significant. Species turnover for all target taxa combined was negligible for two pairs of valleys: Forest Walk and Devil's Hoek ($R = 0.185$, $P = 0.257$), and Yellowwood Forest and van Heyningen's Pass ($R = 0.167$, $P = 0.400$) (Table 2.2). Interestingly one of these pairs comprised the two burned valleys and the other pair comprised two unburned valleys at Injisuthi. Significant species turnover was detected between Forest Walk and Thukela Gorge ($R = 0.963$, $P = 0.029$) and Forest Walk and van Heyningen's Pass ($R = 0.944$, $P = 0.029$) (Table 2.2). Both these comparisons were between a burned and an unburned valley. Although not significant, species turnover was distinct between Forest Walk and Rainbow Gorge ($R = 1.000$, $P = 0.250$), Forest Walk and Yellowwood Forest ($R = 1.000$, $P = 0.250$), Thukela Gorge and Rainbow Gorge ($R = 0.917$, $P = 0.200$), and Rainbow Gorge and van Heyningen's Pass ($R = 1.000$, $P = 0.200$) (Table 2.2).

Similar patterns of species turnover between valleys were found for molluscs and millipedes (Table 2.2). For molluscs, a high level of dissimilarity in species composition was observed between Forest Walk and Thukela Gorge ($R = 0.778$, $P = 0.029$), Forest Walk and Rainbow Gorge ($R = 0.778$, $P = 0.250$), Forest Walk and Yellowwood Forest ($R = 0.889$, $P = 0.250$), Forest Walk and van Heyningen's Pass ($R = 0.889$, $P = 0.029$), Thukela Gorge and Rainbow Gorge ($R = 1.000$, $P = 0.200$), Thukela Gorge and Yellowwood Forest ($R = 1.000$, $P = 0.200$), and Rainbow Gorge and van Heyningen's Pass ($R = 0.917$, $P = 0.200$). For millipedes, distinct species turnover was detected between Forest Walk and Thukela Gorge ($R = 0.806$, $P = 0.029$), Forest Walk and Rainbow Gorge ($R = 1.000$, $P = 0.250$), Forest Walk and Yellowwood Forest ($R = 1.000$, $P = 0.250$), Forest Walk and van Heyningen's Pass ($R = 0.972$, $P = 0.029$), Thukela Gorge and Rainbow Gorge ($R = 0.917$, $p = 0.200$), and Rainbow Gorge and van Heyningen's Pass ($R = 1.000$, $P = 0.200$). For earthworms, centipedes and ants, species turnover was either generally weak or not detected (Table 2.2).

Table 2.1. Turnover of species (β_{sim}) at three spatial scales: within valleys, between valleys, and across the region sampled (n = the number of pairwise comparisons).

Spatial scale		β_{sim}	n	Mean distance (km)
Within a valley				
van Heyningen's Pass (IN)		0.2	6	0.59
Thukela Gorge (RN)		0.2	6	0.61
Forest Walk (RG)		0.3	3	0.27
Devil's Hoek (RN)		0.4	6	1.20
Between valleys				
Yellowwood Forest (IN)	van Heyningen's Pass (IN)	0.2	4	0.85
Thukela Gorge (RN)	van Heyningen's Pass (IN)	0.3	16	65.58
Thukela Gorge (RN)	Yellowwood Forest (IN)	0.3	4	66.40
Rainbow Gorge (CP)	van Heyningen's Pass (IN)	0.3	5	29.35
Devil's Hoek (RN)	van Heyningen's Pass (IN)	0.3	16	66.51
Thukela Gorge (RN)	Devil's Hoek (RN)	0.3	16	2.33
Forest Walk (RG)	van Heyningen's Pass (IN)	0.3	12	65.85
Devil's Hoek (RN)	Yellowwood Forest (IN)	0.3	4	67.36
Thukela Gorge (RN)	Rainbow Gorge (CP)	0.4	4	38.82
Devil's Hoek (RN)	Rainbow Gorge (CP)	0.4	4	39.80
Forest Walk (RG)	Yellowwood Forest (IN)	0.4	3	66.79
Forest Walk (RG)	Devil's Hoek (RN)	0.4	12	9.87
Forest Walk (RG)	Thukela Gorge (RN)	0.4	12	10.28
Forest Walk (RG)	Rainbow Gorge (CP)	0.5	3	39.77
Across the region sampled				
Using pooled species data for valleys		0.3	15	32.98

Table 2.2. Pairwise comparison of species richness between valleys. One-way ANOSIM was based on a ranked dissimilarity matrix of presence/absence data for the 17 forests sampled. F = Forest Walk, T = Thukela Gorge, D = Devil's Hoek, R = Rainbow Gorge, Y = Yellowwood Forest and V = van Heyningen's Pass. Dist = the mean distance between valleys.

Valley pair	Dist (km)	All taxa		Molluscs		Earthworms		Centipedes		Millipedes		Ants	
		R	P	R	P	R	P	R	P	R	P	R	P
Y V	0.9	0.167	0.400	0.125	0.600	x	x	-0.250	1.000	0.292	0.400	0.625	0.400
T D	2.3	0.474	0.029	0.359	0.029	0.268	0.267	0.057	0.314	0.172	0.229	0.000	0.486
F D	9.9	0.185	0.257	-0.222	0.829	-0.500	1.000	0.176	0.229	0.148	0.314	-0.130	0.629
F T	10.3	0.963	0.029	0.778	0.029	0.083	0.800	-0.222	1.000	0.806	0.029	0.398	0.114

R	V	29.4	1.000	0.200	0.917	0.200	0.000	0.750	-0.333	1.000	1.000	0.200	1.000	0.200
T	R	38.8	0.917	0.200	1.000	0.200	0.500	0.200	-0.500	1.000	0.917	0.200	-0.333	0.800
F	R	39.8	1.000	0.250	0.778	0.250	x	x	-0.556	1.000	1.000	0.250	0.778	0.250
D	R	39.8	0.333	0.400	0.375	0.400	1.000	0.333	-0.042	0.800	0.000	0.600	-0.292	1.000
T	V	65.6	0.708	0.029	0.091	0.029	0.333	0.171	-0.125	1.000	0.031	0.286	0.458	0.029
F	V	65.9	0.944	0.029	0.889	0.029	-0.556	1.000	-0.056	0.486	0.972	0.029	0.500	0.029
T	Y	66.4	0.500	0.400	1.000	0.200	x	x	-0.333	1.000	-0.125	0.600	0.042	0.600
D	V	66.5	0.635	0.029	0.693	0.029	-0.417	1.000	0.193	0.200	0.281	0.086	0.505	0.029
F	Y	66.8	1.000	0.250	0.889	0.250	x	x	-0.556	1.000	1.000	0.250	0.333	0.500
D	Y	67.4	0.250	0.400	0.250	0.400	x	x	0.417	0.400	-0.500	1.000	-0.083	0.600

X = No specimens were collected in at least one valley of the pair.

2.4 DISCUSSION

Over the study region 72 species, comprising 31 mollusc, nine earthworm, one onychophoran, six centipede, 12 millipede and 13 ant species, were recorded. The species richness of these target taxa was comparable with that found in similar studies in South African forests. For example, Bourquin (2001) collected six centipede, six millipede and 12 ant species in Afrotropical forest in the KwaZulu-Natal midlands, while Swaye (2004) collected 34 mollusc, five earthworm, eight centipede and 24 millipede species in Afrotropical forest in the Soutpansberg and northern Drakensberg in Limpopo Province. Bourquin (2001) thus collected fewer species (24 compared to 31 species) and Swaye (2004) collected more species (71 compared to 58 species) for the same taxa than in this study. Therefore, at a provincial level, the Drakensberg forests show comparatively high species richness and are consequently important for conservation planning, but this may not hold at a national level, especially for millipedes.

The findings presented here are limited to a small number of forest patches in the Drakensberg Mountains of KwaZulu-Natal, with only one site per forest sampled. Nevertheless, this study provides quantitative, geographically referenced information on the local distribution of forest dwelling invertebrate species. This study also provides a preliminary contribution to understanding how the assemblage composition of flightless invertebrates changes with spatial scale (distance between forests) in Afrotropical forest patches in the region.

2.4.1 *Flightless invertebrate species composition and turnover at different spatial scales*

The first objective of this study was to investigate the variation in flightless invertebrate species composition among sites and species turnover at different spatial scales (i.e. forests separated by increasing distance) to provide insight into the appropriate scale at which conservation and management decisions should be made for the conservation of flightless

invertebrates. Analyses of spatial autocorrelation, community composition and species turnover for all flightless invertebrate target taxa showed that sites separated by distances of <1.3 km (i.e. within valleys) were very similar. Therefore, forest patches within a valley do not necessarily need to be considered individually for conservation and management decisions.

These results concur with general ecological trends. Spatial autocorrelation is a common statistical property of ecological variables detected across geographic space because two sites located near one another are unlikely to be independent from one another (Legendre, 1993; Rosenberg, 2001; Diniz-Filho et al., 2003). Spatial structure was viewed here not as a statistical problem (Legendre, 1993) but as a part of the ecological process under study.

Analysis of species composition among sites in this study suggests that distance (latitude); disturbance (fire history) and mean annual precipitation (MAP) are the most important geographical and environmental processes governing forest invertebrate species composition. These processes need to be considered in management decisions for flightless invertebrate conservation to preserve the full complement of ground dwelling invertebrate diversity.

Turnover relating to distance may be a relatively minor component of regional diversity (Harrison et al., 1992), but in this study it has been demonstrated to significantly contribute to site and local invertebrate diversity. Ground dwelling arthropods in forested north-east New South Wales, Australia also show significant turnover between geographically separated sites (Ferrier et al., 1999). Turnover in species composition (measured here as β_{sim}) was detected at all spatial scales investigated in the Drakensberg, including within valleys, between valleys and across the region sampled. Lennon et al. (2001) reported β_{sim} of 0.1 at the finest scale (10 km quadrat scale) investigated for British birds and so the β_{sim} values reported in this study (0.2 – 0.5) can be considered fairly high. β_{sim} was generally greater between valleys than within valleys suggesting a distance effect on species turnover. However, this distance effect was probably confounded by site-specific environmental variables and level of disturbance (fire history). β_{sim} of unburned sites only was comparatively lower than for burned sites, suggesting that in the absence of disturbance, turnover is in fact low and most species are widespread.

In general, increasing distance between sites increased the significance of species turnover. ANOSIM showed that species turnover was non-significant at small distances between pairs of valleys, whereas species turnover was generally significant at large distances between pairs of valleys. Ferrier et al. (1999) recommend that to represent the diversity of ground dwelling invertebrates in forests, a geographical spread of the reserved proportion of each forest ecosystem to accommodate species turnover within that ecosystem is necessary. Harrison et al. (1992) found that beta diversity increased linearly with distance across a N-S transect in Britain for most of the 15 taxa (including plants, vertebrates and

invertebrates) studied. Higher turnover at greater distances between forests implies that forests throughout the Drakensberg region should be conserved to conserve the high diversity of forest dwelling invertebrates in the region, since invertebrate fauna in the north are different to those in the south.

2.4.2 *Do target taxa show similar patterns of community composition and species turnover?*

Contrary to expectation, target taxa did not all show similar patterns of community composition or species turnover with spatial scale. This may be a result of the different mobility and dispersal abilities of taxa, or differences in life histories between taxa, and it appears that isolation may not be the dominant influence on taxon turnover. Geographical separation affects species composition variably at different spatial scales, and these patterns differ among taxa. Oliver et al. (2004) found that less than 15% of the variation in ground dwelling invertebrate assemblages in New South Wales, Australia, could be explained by geographic separation among sites that showed few environmental differences. Thus the similarity between two biogeographical areas is not necessarily exclusively a function of the distance between them (Brown and Lomolino, 1998). Ferrier et al. (1999) found that ground dwelling arthropods in forested north-east New South Wales were strongly influenced by both environmental variation and geographical separation of sites. This has implications for the scale at which management decisions are made for flightless invertebrate conservation.

The non-significant Monte Carlo test results for earthworms, centipedes and ants suggests that one or more environmental variables driving the species composition of these three taxa in Drakensberg forests may be missing from the set of environmental variables included in the CCA. Alternatively, the non-significant results may reflect the low sample sizes and low species richness recorded for these three taxa. A third possible, but unlikely, explanation is that the species composition of earthworms, centipedes and ants in Drakensberg forests is simply random.

2.4.3 *The importance of conserving dispersal routes in the Drakensberg*

Although not specifically addressed by the objectives of this chapter, the importance of conserving dispersal routes in the Drakensberg needs to be incorporated into recommendations on the appropriate scale at which conservation and management decisions should be made for the conservation of flightless invertebrates because forest patches in the Drakensberg are considered habitat islands in a grassland matrix. This means that forest-dependent species in the Drakensberg have patchy distributions.

In Limpopo Province Afrotropical forests, dispersal corridors include riparian and valley forests, thickets and bush clumps (Geldenhuys and MacDevette, 1989). It is unknown whether dispersal takes place across grassland or via riverine vegetation (*Leucosidea* scrub) within a valley in the Drakensberg. Most forest patches in the Drakensberg have a stream

flowing through the forest, down to the river in the valley below. Some forests sampled were partially connected by riverine vegetation to the valley below these forest patches. It is unknown how many of the species collected in this study occur in the surrounding riverine vegetation, grassland or the forest-grassland ecotone.

Considering only unburned sites, turnover between sites within valleys and between valleys across the region was relatively low, which implies that a common suite of species occurs across the region sampled and dispersal corridors may be important to maintain this pattern. By conserving a forested valley (e.g. by burning fire breaks around forests within a valley to maintain dispersal corridors of unburned vegetation at least within valleys) spatial patterns of species distributions could be conserved. It is therefore important to conserve corridors or dispersal routes between forests in valleys to maintain the long-term viability of Afrotropical forest invertebrate populations. Future studies should investigate dispersal routes and incorporate a variety of vegetation types to provide a wider knowledge of the system.

2.4.4 *Forest patch size*

Patch size is another important consideration for recommendations on the appropriate scale at which conservation and management decisions should be made for the conservation of flightless invertebrates in the Drakensberg because patch size influences species distributions and number. Larger habitat patches generally support greater habitat diversity and therefore greater biodiversity, as well as larger and more persistent populations (Saunders et al., 1991). In a similar study, Bourquin (2001) recommended that in afforested landscapes the largest intact forest fragments should be conserved to preserve overall epigaeic invertebrate species richness. However, Swaye (2004) found that conserving only the largest forest patches would not effectively protect invertebrate species in Limpopo Province where no single forest patch studied could be excluded from conservation if all aspects of diversity are to be conserved. Small forests may act as "stepping stones" (Fahrig and Merriam, 1994; Ingham and Samways, 1996; Primack, 2000) for dispersal between larger forest patches, and are therefore important components of the landscape. In this study, forest patch size appears not to be a strong determinant of invertebrate species composition among sites, and several of the smallest areas sampled supported comparatively high species richness, however, the larger forests may be under sampled. It is unknown how many of these species also occur in forest ecotones and grassland. However, for small-bodied animals such as invertebrates, which may spend their entire lives in a single log, even forests with an area of one hectare might be sustainable habitats. Therefore, small forest patches have conservation value and the ecological role and biodiversity value of small forest patches should not be ignored (Lawes et al., 2004).

2.4.5 *Fire history*

This study was not designed to test the effect of fire on forest invertebrates, but has shown that forest fires have potentially detrimental effects on invertebrate community composition, even 18 months after burning. Fire history appears to be an important determinant of species richness, species composition and species turnover among forests. If fire is a stochastic event that removes species at random, with unpredictable effects, then dispersal may be important to allow species to recolonize after such events and potential dispersal corridors should be maintained in the landscape. Fire acts as a disturbance event (Hobbs and Huenneke, 1992; Moretti et al., 2006) that opens up the canopy and ground layer, decreases leaf litter, alters the pH and nutrient status of forest soils, increases evaporative losses and results in generally drier conditions on the forest floor (Granger, 1984). Fire appears to lower invertebrate species richness and increase species turnover between forests within and between valleys. Many species that are highly fire sensitive may already have been eradicated from large areas of the Drakensberg such that species that are still present may only represent a subset of the original fauna. Furthermore, fire affects invertebrates to varying degrees. Slow-moving, ground dwelling invertebrates that are restricted to forests are probably extremely vulnerable to fire (Collet and Neumann, 2003). Molluscs, onychophorans, centipedes and millipedes are likely to use refugia such as rocks, logs, or trees and many are able to burrow into the soil or into crevices at the roots of shrubs to avoid fire when possible (Tainton and Mentis, 1984). Forests also provide refugia for both invertebrates and vertebrates during and after grassland fires. The current management strategy for burning in the Maloti-Drakensberg Bioregion is to exclude fire from forests and, where possible, precautions are taken to do so. Unfortunately, wildfires are fairly common and unpredictable in the Drakensberg, and fires do occasionally reach the centre of mature forest patches (von Maltitz et al., 2003). The effect of fire on forest invertebrates requires further study. An opportunistic study comparing the post-burn faunal composition of nearby burned and unburned forests is recommended to further our understanding of the immediate impact of fire on forest invertebrates, and to track the recolonization and succession of burned forest over time.

2.4.6 *Additional future research*

Forest patches outside of protected areas within the Drakensberg Mountains may have conservation value and could potentially be surveyed in a rapid and cost efficient manner. These forests may be of higher conservation concern than forests under formal protection because they face higher levels of threats. However, forests outside of protected areas would only be worth protecting if they support populations of species not found in protected areas and/or populations of rare or threatened species. The invertebrate diversity of forests outside of protected areas in the Drakensberg is unknown, as these forests have not yet

been quantitatively surveyed. For example, the Upper Thukela region between Cathedral Peak and Royal Natal National Park is not currently under formal protection and does not form part of the uKhahlamba-Drakensberg Park (Ezemvelo KZN Wildlife, 2005). Forests in this region may well support populations of critically endangered invertebrates, but we lack empirical data to support this speculation. A conservation plan for the Afrotropical forests of the Maloti-Drakensberg Bioregion might need to take into account a more extensive data set from forests throughout the Bioregion, if they prove to be valuable for invertebrate conservation.

2.4.7 Conclusion

Although generally small and fragmented, the Afrotropical forest patches of the KwaZulu-Natal Drakensberg are of high conservation value for their wealth of invertebrate species. Species turnover was detected at all spatial scales investigated in the Drakensberg, namely within valleys (where patches are only a few hundred meters apart), between valleys and across the region sampled (over a distance of nearly 70 km). Spatial patterns of diversity therefore must be considered in management decisions for forest conservation, and as far as possible, all Drakensberg forest patches should be conserved to conserve the high diversity of the region.

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Appendix 2a. Location and number of species recorded for each site. MAP = mean annual precipitation. RG = Rugged Glen Nature Reserve, RN = Royal Natal National Park, CP = Cathedral Peak and IN = Injisuthi. All = all taxa combined, Mo = molluscs, Ea = earthworms, On = onychophorans, Ce = centipedes, Mi = millipedes and An = ants.

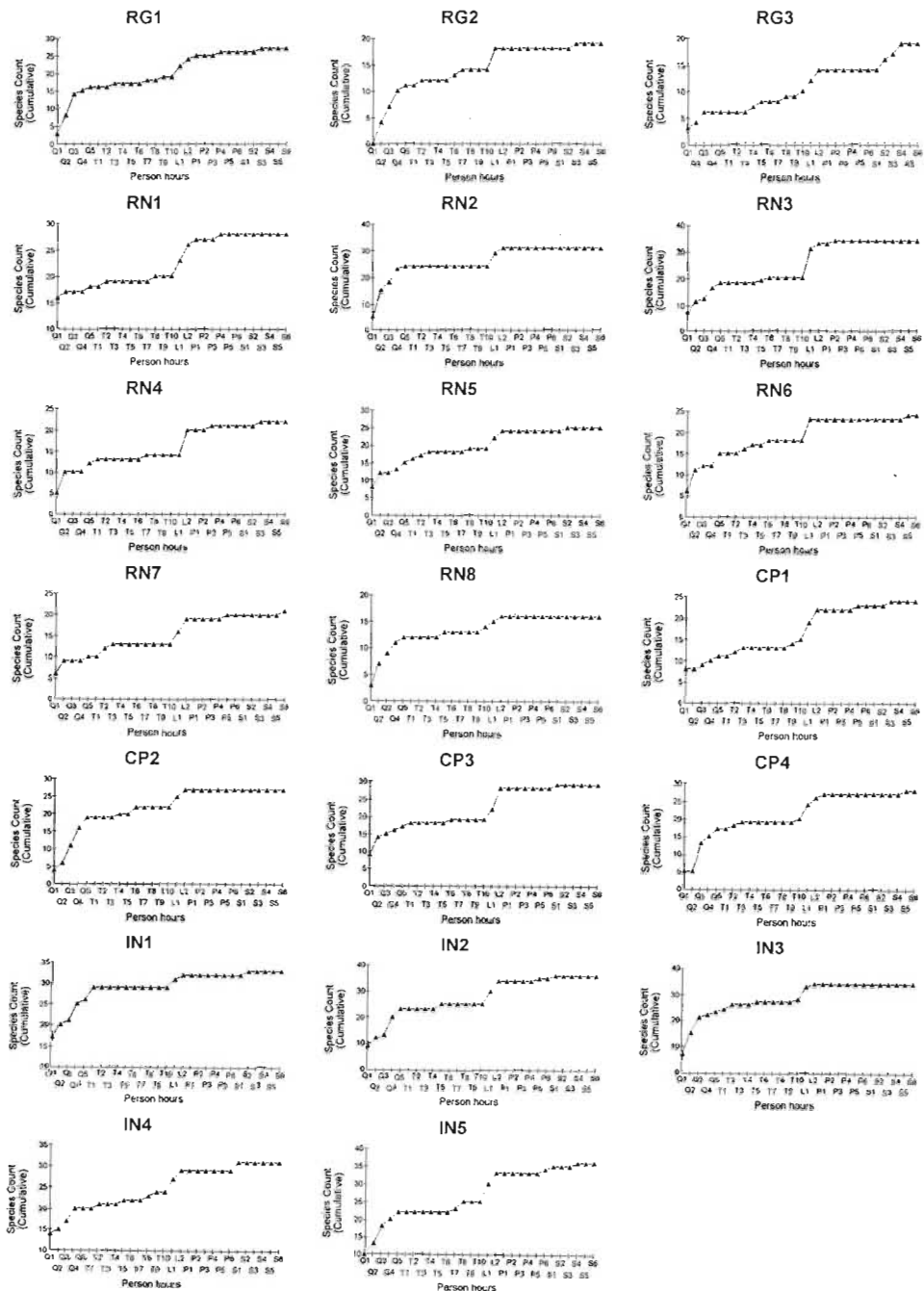
Site	Valley	GPS Co-ordinates (WGS84)	Altitude (m a.s.l.)	Aspect	Area (ha)	MAP (mm)	Fire history	Number of species						
								All	Mo	Ea	On	Ce	Mi	An
RG 1	Forest Walk	28.6619 S 28.9926 E	1400	S	3.46	909	burned	27	7	1	0	6	5	8
RG 2	Forest Walk	28.6620 S 28.9912 E	1400	S	2.7	878	burned	19	6	0	0	3	4	6
RG 3	Forest Walk	28.6616 S 28.9885 E	1400	S	1.14	878	burned	19	4	0	0	4	5	6
RN 1	Thukela Gorge	28.7316 S 28.9134 E	1700	SSE	12.5	1327	unburned	28	13	1	0	4	8	2
RN 2	Thukela Gorge	28.7305 S 28.9180 E	1600	S	14	1327	unburned	30	17	1	0	4	7	1
RN 3	Thukela Gorge	28.7292 S 28.9212 E	1620	S	7.64	1327	unburned	35	17	2	0	6	7	3
RN 4	Thukela Gorge	28.7276 S 28.9237 E	1600	S	4.26	1327	unburned	22	11	1	0	2	5	3
RN 5	Devil's Hoek	28.7102 S 28.9182 E	1700	SE	35.7	1225	burned	24	10	0	0	5	5	4
RN 6	Devil's Hoek	28.7105 S 28.9244 E	1620	SSE	12	1225	burned	24	8	1	0	5	5	5
RN 7	Devil's Hoek	28.7089 S 28.9287 E	1620	S	11.4	1142	burned	20	9	0	0	6	1	4
RN 8	Devil's Hoek	28.7111 S 28.9313 E	1550	WSW	8.28	1142	burned	16	5	2	0	4	2	3
CP 1	Rainbow Gorge	28.9619 S 29.2189 E	1500	S	*	1167	unburned	22	11	1	0	5	2	3
CP 2	Rainbow Gorge	28.9619 S 29.2213 E	1550	S	*	1167	unburned	25	10	2	0	5	7	1
CP 3	Rainbow Gorge	28.9581 S 29.2207 E	1550	S	21.8	1167	unburned	30	15	3	0	5	5	2
CP 4	Rainbow Gorge	28.9601 S 29.2252 E	1600	S	*	1167	unburned	29	11	1	1	5	7	4
IN 1	Yellowwood Forest	29.1197 S 29.4360 E	1500	SSW	1.41	1022	unburned	33	18	0	0	4	8	3
IN 2	van Heyningen's Pass	29.1080 S 29.4334 E	1650	SSW	2.46	1076	unburned	34	15	2	1	6	7	3
IN 3	van Heyningen's Pass	29.1100 S 29.4390 E	1600	S	5.28	1022	unburned	34	17	0	0	4	9	4
IN 4	van Heyningen's Pass	29.1100 S 29.4390 E	1600	SSW	3.92	1022	unburned	31	14	1	0	4	7	5
IN 5	van Heyningen's Pass	29.1077 S 29.4297 E	1650	S	2.41	1076	unburned	36	16	3	0	5	8	4

* Four sites within one continuous forest, Rainbow Gorge Valley, Cathedral Peak. These sites were located approximately 200 m apart within Rainbow Gorge Forest.

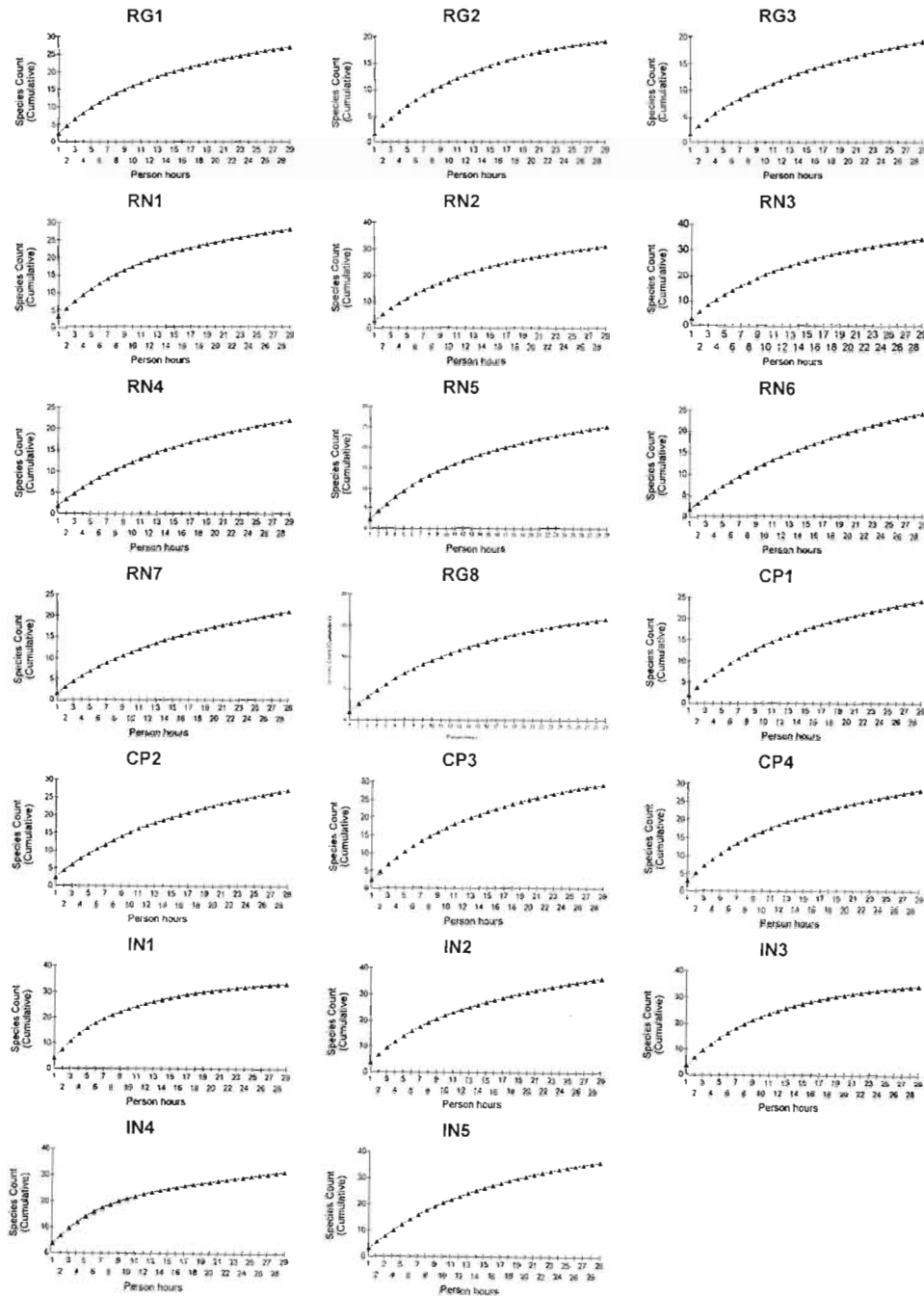
Appendix 2b. Checklist of tree species sampled in tree beats. Trees were identified in the field using Pooley (2003).

Family	Genus	species	Authority	English common name
Anacardiaceae	<i>Rhus</i>	<i>dentata</i>	Thunb.	Nana-berry
Anacardiaceae	<i>Rhus</i>	<i>montana</i>	Diels	Drakensberg Karree
Apocynaceae	<i>Carissa</i>	<i>bispinosa</i>	(L.) Desf. Ex Brenan	Forest Num-num
Aquifoliaceae	<i>Ilex</i>	<i>mitis</i>	(L.) Radlk.	Cape Holly
Balanitaceae	<i>Clausena</i>	<i>anisata</i>	(Wild.) Hook.f. ex Benth.	Horsewood
Celastraceae	<i>Maytenus</i>	<i>peduncularis</i>	(Sond.) Loes.	Cape Blackwood
Celastraceae	<i>Maytenus</i>	<i>undata</i>	(Thunb.) Blakelock	Koko Tree, South African Holly
Ebenaceae	<i>Diospyros</i>	<i>whyteana</i>	(Hiern) F. White	Bladder-nut, Blackbark
Ebenaceae	<i>Euclea</i>	<i>crispa</i>	(Thunb.) Guerke	Blue Guarri
Flacourtiaceae	<i>Trimeria</i>	<i>grandifolia</i>	(Hochst.) Warb.	Wild Mulberry
Icacinaceae	<i>Cassinopsis</i>	<i>ilicifolia</i>	(Hochst.) Kuntze	Lemon Thorn
Lauraceae	<i>Cryptocarya</i>	<i>woodii</i>	Engl.	Cape Quince, Bastard Camphor Tree
Oliniaceae	<i>Olinia</i>	<i>emarginata</i>	Burr Davy	Mountain Hard Pear
Podocarpaceae	<i>Podocarpus</i>	<i>henkelii</i>	Stapf ex Dallim. Jacq.	Henkel's Yellowwood
Podocarpaceae	<i>Podocarpus</i>	<i>latifolius</i>	(Thunb.) R.Br. Ex Mirb.	Real Yellowwood
Rubiaceae	<i>Canthium</i>	<i>ciliatum</i>	(Klotzsch) Kuntze	Hairy Turkey-berry, Dwarf Turkey-berry
Ulmaceae	<i>Celtis</i>	<i>africana</i>	N.L.Burm.	White Stinkwood

Appendix 2c. Sample-based field species-accumulation curves of all target taxa combined (72 species) for each site sampled in the Drakensberg. The x-axes represent the number of person hours taken to collect and process each sampling replicate. Q = one 2 x 2 m active search quadrat, T = five tree beats from one tree, L = one 2 l leaf litter sample, P = one 125 ml pitfall trap, and S = one 300 ml soil sample. RG = Rugged Glen Nature Reserve, RN = Royal Natal National Park, CP = Cathedral Peak and IN = Injisuthi. The numbers represent sites sampled within each reserve.



Appendix 2d. Sample-based randomized species-accumulation curves of all target taxa combined (72 species) for each site sampled in the Drakensberg. The x-axes represent the number of person hours taken to collect and process each sampling replicate. RG = Rugged Glen Nature Reserve, RN = Royal Natal National Park, CP = Cathedral Peak and IN = Injisuthi. The numbers represent sites sampled within each reserve.



Appendix 2e. List of mollusc, earthworm, onychophoran, centipede, millipede and ant species collected. Mollusc endemicity is based on the eight categories used by Herbert and Kilburn (2004). Millipede endemicity is based on the four categories used by Hamer and Slotow (2002).

Sp.	Order	Family	Genus	species	Authority	Area of endemism
Class Gastropoda						
1	Neritopsina	Hydrocenidae	<i>Hydrocena</i>	<i>noticola</i>	Benson, 1856	South Africa
2	Architaenioglossa	Cyclophoridae	<i>Chondrocyclus</i>	<i>ispingoensis</i>	(Sturany, 1898)	South Africa
3	Eupulmonata	Pupillidae	<i>Lauria</i>	<i>dadion</i>	(Benson, 1864)	South Africa
4	Eupulmonata	Orculidae	<i>Fauxulus</i>	<i>glanvilleanus (darglensis)</i>	(Ancey, 1888)	KZN-Eastern Cape
5	Eupulmonata	Orculidae	<i>Fauxulus</i>	<i>mcbeanianus</i>	Melville and Ponsonby, 1901	KZN
6	Eupulmonata	Orculidae	<i>Fauxulus</i>	sp.		
7	Eupulmonata	Vertiginidae	<i>Pupisoma</i>	<i>harpula</i>	(Reinhardt, 1886)	Afro-Asian
8	Eupulmonata	Vertiginidae	<i>Truncatellina</i>	<i>sykesii</i>	(Melville and Ponsonby, 1893)	southern Africa
9	Eupulmonata	Clausiliidae	<i>Macroptychia</i>	<i>africana</i>	(Melville and Ponsonby, 1899)	South Africa
10	Eupulmonata	Achatinidae	<i>Archachatina</i>	sp.		
11	Eupulmonata	Streptaxidae	<i>Gulella</i>	<i>juxtident</i>	(Melville and Ponsonby, 1899)	KZN
12	Eupulmonata	Streptaxidae	<i>Gulella</i>	<i>maniae</i>	(Melville and Ponsonby, 1892)	KZN-Eastern Cape
13	Eupulmonata	Streptaxidae	<i>Gulella</i>	sp.		
14	Eupulmonata	Rhytidae	<i>Nata</i>	<i>vernicaosa</i>	(Krauss, 1848)	southern Africa
15	Eupulmonata	Rhytidae	<i>Natalina</i>	sp.		
16	Eupulmonata	Valloniidae	<i>Acanthinula</i>	sp.		
17	Eupulmonata	Charopidae	<i>Afrodonta</i>	<i>novemlamellaris</i>	(Burnup, 1912)	central and southern Africa
18	Eupulmonata	Charopidae	<i>Trachysystis</i>	<i>contabulata</i>	Connolly, 1932	KZN-Transkei
19	Eupulmonata	Charopidae	<i>Trachysystis</i>	<i>ectima</i>	(Melville and Ponsonby, 1899)	KZN
20	Eupulmonata	Charopidae	<i>Trachysystis</i>	<i>rudicostata</i>	Connolly, 1923	central and southern Africa
21	Eupulmonata	Charopidae	<i>Trachysystis</i>	<i>subpinguis</i>	Connolly, 1922	South Africa
22	Eupulmonata	Charopidae	<i>Trachysystis</i>	<i>glanvilliana</i>	(Ancey, 1893)	eastern South Africa
23	Eupulmonata	Charopidae	<i>Trachysystis</i>	<i>venatorum</i>	Connolly, 1932	South Africa
24	Eupulmonata	Helicariionidae	<i>Kaliella</i>	<i>euconuloides</i>	Melville and Ponsonby, 1908	KZN
25	Eupulmonata	Euconulidae	<i>Afroconulus</i>	<i>diaphanus</i>	(Connolly, 1922)	central and southern Africa
26	Eupulmonata	Urocyliidae	<i>Sheldonia</i>	<i>transvaalensis</i>	(Craven, 1880)	South Africa
27	Eupulmonata	Achatinidae	<i>Archachatina</i>	<i>dimidiata</i>	(Smith, 1878)	South Africa
28	Eupulmonata	Vertiginidae	<i>Pupisoma</i>	<i>orca</i>	(Benson, 1850)	Afro-Asian
29	Eupulmonata	Pupillidae	? <i>Pupilla</i>	<i>fontana</i>	(Krauss, 1848)	central and southern Africa
30	Eupulmonata	Charopidae	<i>Trachysystis</i>	sp.		
264	Eupulmonata	Chlamydephoridae	<i>Chlamydephorus</i>	<i>burnupi</i>	Smith, 1892	eastern South Africa
Class Oligochaeta						
254	Haplotaaxida	Acanthodrilidae	<i>Dichogaster</i>	sp.		
255	Haplotaaxida	Acanthodrilidae	<i>Parachilota</i>	sp.1		
256	Haplotaaxida	Acanthodrilidae	<i>Parachilota</i>	sp.2		
257	Haplotaaxida	Enchytraeidae		sp.3		
258	Haplotaaxida	Lumbricidae	<i>Octolasion</i>	<i>lacteum</i>	(Oerley, 1885)	
259	Haplotaaxida	Lumbricidae	<i>Apporectodea</i>	<i>rosea</i>	(Savigny, 1826)	
260	Haplotaaxida	Lumbricidae	<i>Dendrodilus</i>	<i>rubidus</i>	(Savigny, 1826)	
261	Haplotaaxida	Megascolicidae	<i>Amyntas</i>	sp.		
262	Opisthopora	Microchaetidae	<i>Proandricus</i>	sp.		
Class Onychophora						
263	Onychophora	Onychophora	<i>Opisthopatus</i>	<i>cinctipes</i>	Purcell, 1899	
Class Chilopoda						
45	Geophilomorpha	Geophilidae	<i>Rhysida</i>	<i>afra (afra)</i>	(Peters, 1855)	
47	Geophilomorpha	Geophilidae	<i>Rhysida</i>	sp.2		
48	Geophilomorpha	Geophilidae	<i>Rhysida</i>	sp.1		
49	Lithobiomorpha	Henicopidae	<i>Paralamyctes</i>	<i>spenceri</i>	Pocock, 1902	
50	Lithobiomorpha	Henicopidae	<i>Lamyctes</i>	<i>africana</i>	(Porat, 1971)	
51	Lithobiomorpha	Henicopidae	<i>Lamyctes</i>	sp.		
Class Diplopoda						
32	Sphaerotheirida	Sphaerotheiridae	<i>Sphaerotherium</i>	<i>perbrincki</i>	Schubart, 1958	Site
33	Sphaerotheirida	Sphaerotheiridae	<i>Sphaerotherium</i>	<i>dorsale</i>	(Gervais, 1847)	South Africa
34	Sphaerotheirida	Sphaerotheiridae	<i>Sphaerotherium</i>	<i>mahaum</i>	Schubart, 1958	Site
35	Sphaerotheirida	Sphaerotheiridae	<i>Sphaerotherium</i>	sp.		
36	Polydesmida	Dalodesmidae	<i>Gnomeskelus</i>	sp.		
37	Polydesmida	Gomphodesmidae	<i>Ulodesmus</i>	<i>simplex</i>	Lawrence, 1953	Site
38	Polydesmida	Gomphodesmidae	<i>Gnomeskelus</i>	<i>montivagus</i>	Verhoeff, 1939	Local
39	Polydesmida	Gomphodesmidae	<i>Gnomeskelus</i>	<i>attemsii</i>	Verhoeff, 1939	Regional
40	Spirostreptida	Odontopygidae	<i>Spinotarsus</i>	sp.2		
41	Spirostreptida	Odontopygidae	<i>Spinotarsus</i>	sp.1		
43	Spirostreptida	Spirostreptidae	<i>Doratogonus</i>	<i>montanus</i>	Hamer, 2000	Regional
44	Polyzoniida	Siphonotidae	<i>Rynchomecogaster</i>	<i>lawrencei</i>	Verhoeff, 1939	Site
Class Insecta						
53	Hymenoptera	Formicidae		sp.1		
54	Hymenoptera	Formicidae		sp.2		
55	Hymenoptera	Formicidae		sp.3		
56	Hymenoptera	Formicidae		sp.4		
57	Hymenoptera	Formicidae		sp.5		
58	Hymenoptera	Formicidae		sp.6		
59	Hymenoptera	Formicidae		sp.7		
60	Hymenoptera	Formicidae		sp.8		
61	Hymenoptera	Formicidae		sp.9		
62	Hymenoptera	Formicidae		sp.10		
63	Hymenoptera	Formicidae		sp.11		
64	Hymenoptera	Formicidae		sp.12		
65	Hymenoptera	Formicidae		sp.13		

Appendix 2f. Abundance data for the 72 species recorded across the 20 sites sampled. RG = Rugged Glen Nature Reserve, RN = Royal Natal National Park, CP = Cathedral Peak and IN = Injisuthi. The numbers represent sites sampled within each reserve.

Sp.	Class	RG 1	RG 2	RG 3	RN 1	RN 2	RN 3	RN 4	RN 5	RN 6	RN 7	RN 8	CP 1	CP 2	CP 3	CP 4	IN 1	IN 2	IN 3	IN 4	IN 5
1	Gastropoda	0	0	0	1	67	11	30	0	0	0	0	7	2	6	3	4	76	88	0	11
2	Gastropoda	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	21	1	12	18	10
3	Gastropoda	0	0	0	2	3	3	1	1	0	0	0	1	0	1	0	2	2	3	0	8
4	Gastropoda	0	0	0	9	35	2	0	3	3	0	0	5	0	4	2	11	34	5	2	8
5	Gastropoda	0	0	0	5	10	3	0	0	2	0	0	1	4	10	3	22	28	6	14	0
6	Gastropoda	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7	Gastropoda	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2	2	10	5	0
8	Gastropoda	0	2	0	1	0	1	9	0	0	0	0	0	0	1	0	4	10	21	9	4
9	Gastropoda	0	0	0	28	9	9	0	0	0	0	0	1	3	0	2	9	2	0	5	0
10	Gastropoda	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	6	7	0	0	1
11	Gastropoda	2	2	0	23	31	9	4	2	1	1	0	0	0	0	0	0	0	0	0	0
12	Gastropoda	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	2	2	5	2	5
13	Gastropoda	1	0	0	0	1	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0
14	Gastropoda	1	0	0	0	5	3	0	1	0	0	0	0	0	0	0	0	0	0	0	0
15	Gastropoda	0	0	0	0	0	0	0	0	0	0	0	0	0	4	2	0	0	0	0	0
16	Gastropoda	2	0	0	1	8	10	0	1	0	3	0	1	2	0	3	2	6	16	27	5
17	Gastropoda	0	0	0	0	5	7	1	0	0	1	0	0	1	0	0	0	0	6	4	32
18	Gastropoda	1	8	3	0	2	0	0	0	4	3	4	3	0	1	1	4	9	20	1	5
19	Gastropoda	4	2	1	10	9	5	22	25	19	15	2	0	1	0	0	21	0	1	2	2
20	Gastropoda	0	0	2	12	14	11	4	0	3	1	0	2	0	2	4	6	11	14	21	17
21	Gastropoda	0	0	2	2	14	8	2	2	0	1	1	1	0	1	9	13	0	1	12	0
22	Gastropoda	0	1	0	0	0	0	0	3	0	1	0	1	4	3	1	1	0	0	0	0
23	Gastropoda	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24	Gastropoda	2	0	0	2	13	4	4	0	1	1	0	2	6	0	5	11	87	19	22	23
25	Gastropoda	0	2	0	0	0	0	0	4	0	1	0	0	1	5	0	0	1	3	2	1
26	Gastropoda	0	0	0	1	5	2	1	11	9	0	1	0	2	5	0	0	0	0	0	0
27	Gastropoda	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2
28	Gastropoda	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29	Gastropoda	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30	Gastropoda	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
264	Gastropoda	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
254	Oligochaeta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0
255	Oligochaeta	6	0	0	2	0	1	0	0	1	0	3	0	11	8	5	0	24	0	5	3
256	Oligochaeta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
257	Oligochaeta	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
258	Oligochaeta	0	0	0	0	0	0	0	0	0	0	0	0	50	0	0	0	0	0	0	0
259	Oligochaeta	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
260	Oligochaeta	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0
261	Oligochaeta	0	0	0	0	0	0	0	0	0	0	0	0	0	38	0	0	0	0	0	296
262	Oligochaeta	0	0	0	0	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0
263	Onychophora	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
45	Chilopoda	2	5	3	1	5	12	2	2	6	5	1	3	5	3	0	5	1	6	9	1
47	Chilopoda	6	0	2	7	7	1	0	5	5	9	10	5	0	1	11	8	22	6	11	4
48	Chilopoda	3	4	2	4	7	5	0	3	0	2	0	5	19	3	13	3	13	4	1	1
49	Chilopoda	1	0	0	0	0	1	2	0	4	3	1	5	3	7	12	0	1	0	0	1
50	Chilopoda	12	8	12	52	31	29	0	15	4	5	17	7	26	26	12	42	24	26	24	9
51	Chilopoda	2	0	0	0	0	1	0	1	2	5	0	0	1	0	1	0	1	0	0	0
32	Diplopoda	0	0	0	39	7	21	23	3	7	0	0	0	10	3	1	111	7	3	0	18
33	Diplopoda	6	4	3	36	92	104	79	0	3	0	0	0	0	0	0	6	9	9	1	2
34	Diplopoda	2	1	5	1	4	6	45	0	0	4	7	2	5	0	8	138	1	41	58	9
35	Diplopoda	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	12	0	7	0	0
36	Diplopoda	1	2	0	9	11	7	5	4	1	0	0	9	2	6	43	2	42	30	34	10
37	Diplopoda	0	0	0	12	0	3	0	0	0	0	0	9	0	1	0	21	11	62	2	0
38	Diplopoda	0	0	0	7	1	0	0	1	1	0	0	0	1	2	3	4	16	7	30	7
39	Diplopoda	0	0	0	5	2	2	0	1	0	0	0	1	0	1	18	1	4	11	11	0
40	Diplopoda	0	0	0	1	0	0	1	5	6	0	0	0	0	0	0	1	0	0	0	1
41	Diplopoda	6	0	1	0	0	0	0	0	0	0	2	0	1	0	0	0	0	3	0	0
42	Diplopoda	1	3	3	0	1	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0
43	Diplopoda	0	0	0	0	0	0	0	0	0	0	0	0	4	15	0	0	0	0	0	0
44	Diplopoda	2	5	3	1	5	12	2	2	6	5	1	3	5	3	0	5	1	6	9	1
53	Insecta	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
54	Insecta	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
55	Insecta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
56	Insecta	94	7	15	1	10	2	4	23	45	10	24	5	5	1	39	18	4	9	17	17
57	Insecta	8	37	14	2	0	0	13	6	14	10	2	2	0	1	1	16	0	2	1	3
58	Insecta	32	12	1	0	0	1	1	10	2	0	0	0	0	0	1	0	1	5	2	1
59	Insecta	11	3	0	0	0	0	0	0	0	0	0	1	0	0	0	2	11	3	1	1
60	Insecta	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
61	Insecta	0	0	76	0	0	0	0	0	0	22	0	0	0	0	19	0	0	0	2	0
62	Insecta	1	0	35	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
63	Insecta	21	2	0	0	0	21	0	0	0	1	19	0	0	0	0	0	0	0	0	0
64	Insecta	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
65	Insecta	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

3 AN ASSESSMENT OF SEASON, TAXA AND SAMPLING METHODS FOR MEASURING AND MONITORING FOREST INVERTEBRATES

ABSTRACT

The diversity and complexity of invertebrate communities usually result in their exclusion from conservation activities. However, the importance of invertebrates in ecosystems and their high levels of diversity and endemism mean that invertebrates should be included in biodiversity assessments and monitoring programmes. There are few accepted protocols relating to the season, sampling methods or invertebrate taxa for inclusion in assessment and monitoring programmes. Here I make recommendations for these issues for flightless invertebrates in Afrotropical forest in the Drakensberg, South Africa. Three Afrotropical forests were sampled at Injisuthi during March, June, September and December 2004. Sampling methods included soil and leaf litter samples, pitfall traps, active searching of quadrats and tree beating. Target taxa (Mollusca, Annelida, Diplopoda, Chilopoda and Formicidae) were sorted to morphospecies and identified to species by taxonomic experts. "Best practice" approaches to biodiversity assessment and monitoring based on season, taxa and sampling methods were assessed, and the recommendations for monitoring based on seasonal sampling at Injisuthi were tested using eight Afrotropical forests at Royal Natal National Park. Species richness differed between wet (March and December) and dry (June and September) season months. Community structure of flightless invertebrates changed seasonally and among sites clustered by month and not by location. It is recommended that invertebrate sampling take place only during the wet season. Molluscs met most of the suggested criteria for surrogates and diversity indicators in terms of flightless invertebrates in Afrotropical forest. Active search quadrats and litter samples were the most effective and efficient sampling methods.

3.1 INTRODUCTION

A systematic approach to conservation includes the measurement and assessment of biodiversity features for prioritizing areas and adaptive management of priority areas, involving monitoring the impacts of management or disturbance (Margules and Pressey, 2000). There is, however, much current debate on the use of surrogate taxa or features for assessing biodiversity (Pearson, 1994; Andelman and Fagan, 2000), and protocols for monitoring using indicator taxa are not well established for terrestrial ecosystems (McGeoch, 1998; Andersen, 1999).

Invertebrates are especially poorly represented in conservation activities largely because of their enormous abundance and diversity, and the lack of appropriate information

for most taxa. Their importance in ecosystems (in decomposition, nutrient recycling, pollination etc.), high levels of endemism (Ponder, 1999) and apparent responsiveness to environmental change (Didham and Springate, 2003) mean that invertebrates should be included in biodiversity conservation programmes. Achieving this presents several challenges. Most invertebrates are short-lived and many have complex life cycles. This means that adults are often absent from habitats for extended periods, so diversity is likely to change over shorter spatial and temporal periods than for woody vegetation or vertebrates. There are few generally accepted, standardized sampling methods or protocols for terrestrial invertebrate taxa and the reaction of most taxa to environmental disturbance, natural or anthropogenic. These problems have to be addressed before invertebrates can be effectively included in conservation programmes and monitoring activities.

3.1.1 Seasonality in invertebrate populations

While studies of forest invertebrates in South and Central America (Guerrero et al., 2003; Palacios-Vargas and Castaño-Meneses, 2003; Stuntz et al., 2003), Cameroon (De Winter and Gittenberger, 1998), Mount Kenya (Tattersfield et al., 2001), the coastal forests of East Africa (Burgess et al., 1999) and western Uganda (Wagner, 2003) all show higher abundance during the wet season than the dry, few studies have examined seasonal effects on community structure. This has relevance to both biodiversity assessment and monitoring. Species turnover within seasons is also important to assess.

Seasonal changes in invertebrate diversity need to be considered to standardize monitoring programmes and to allow comparisons of sampling carried out at different times of the year for biodiversity assessments. Sampling should take place when most surrogate or indicator species are present in the adult phase of their life cycle (for accurate species identification), and species not present or detected are not threatened or highly endemic. Species with short adult life cycles or short periods of surface activity may go undetected if sampling takes place at an inappropriate time of year. It is also important to determine whether different communities occur in the dry and wet seasons as this could affect management decisions.

Taxa suitable for use in biodiversity assessment and monitoring ideally should not show large seasonal differences in species composition. However, in strongly seasonal environments, seasonal differences in species composition are expected. In such cases, seasonal differences need to be quantified to reliably interpret other criteria for choosing surrogates for biodiversity assessment and indicators for monitoring.

3.1.2 Invertebrate sampling methods

The efficiency, relative merits and time constraints of sampling methods must be carefully considered for biodiversity assessment and monitoring programmes. Sampling methods for

biodiversity assessment should maximise the number of species sampled, while sampling methods for long-term monitoring programmes should be standardized to ensure data are comparable (Sørensen et al., 2002). Several authors advocate the use of a combination of active and passive sampling methods to reduce misinterpretation of the composition of invertebrate assemblages (Mesibov et al., 1995; Green, 1999; Slotow and Hamer, 2000). There is little local consensus as to which quantitative sampling methods are best for the most commonly collected invertebrate taxa, especially forest dwelling invertebrates.

3.1.3 *Surrogate taxa for biodiversity assessment*

Given limited resources, baseline studies to identify suitable surrogate taxa for biodiversity assessments are necessary (Margules and Pressey, 2000). Two types of surrogates are used in conservation planning: taxonomic (where one taxon is used to reflect the diversity of a wider range of taxa) and environmental (land classes as surrogates for taxa) (Oliver et al., 2004). This study focuses on the former type of surrogate. Surrogate taxa have also been referred to as biodiversity indicators (McGeoch, 1998) since they indicate the diversity of a wider range of taxa within a habitat, but to avoid possible semantic confusion, I use the term “surrogate” when referring to biodiversity assessment. Biodiversity assessments should focus on biogeographically informative taxa (Kremen et al., 1993). Surrogate taxa for biodiversity assessments should therefore:

- 1) not be strongly influenced by seasonal changes;
- 2) have relatively high species richness and abundance;
- 3) include both rare and common species;
- 4) show high levels of endemism at the local scale;
- 5) have a well known and stable taxonomy;
- 6) be easy to find and identify; and
- 7) represent other invertebrate taxa (Pearson, 1994).

Flightless invertebrates such as molluscs, earthworms, onychophorans, centipedes, millipedes and ants are potentially suitable surrogate taxa for biodiversity assessments in Afrotropical forests in the Drakensberg because they meet most of Pearson's (1994) a priori criteria. These taxa have limited dispersal ability and consequently exhibit high levels of endemism in Drakensberg forests (Ezemvelo KZN Wildlife, 2005), relatively well known taxonomy, and are easily observed. Here I investigate whether these target taxa meet the first and last criteria and investigate their suitability for use as surrogates in biodiversity assessments for flightless invertebrate conservation.

3.1.4 *Indicator taxa for monitoring*

Monitoring is the repeated measurement of biological entities or processes over time to track changes in the biological integrity of ecosystems (Heywood and Baste, 1995; Andersen et

al., 2004). Taxa used in monitoring programmes are referred to as “indicator” taxa (McGeoch, 1998). Six criteria should be considered when choosing indicator taxa for monitoring:

- 1) their distribution and diversity should be relatively well known;
- 2) they must be functionally important in ecosystems;
- 3) they must show sensitivity to environmental change;
- 4) be easily sampled, sorted and identified;
- 5) their response to environmental change must be reliably interpreted; and
- 6) they must accurately reflect the responses of other taxa (Andersen, 1999).

McGeoch (1998) defines a biological indicator as a species or group of species that: (1) readily reflects the abiotic or biotic state of an environment; (2) represents the impact of environmental change on a habitat, community or ecosystem; or (3) is indicative of the diversity of a subset of taxa within an area. Based on this definition, biological indicators can be divided into three categories: environmental, ecological and biodiversity indicators. Biological indicators play a key role in conservation planning and management (Andersen, 1999).

There is a widespread recognition of the value of terrestrial invertebrates as biological indicators (Andersen et al., 2002; Andersen and Majer, 2004). Taxa including ants, beetles, butterflies, cicadas, flies, grasshoppers and spiders have been promoted as indicators of disturbance (Andersen, 1999 and references therein). Invertebrates are useful biological indicators because they are extremely diverse (Colwell and Coddington, 1994; McGeoch, 1998). Flightless invertebrates are highly sensitive to changes in the environment (Kotze and Samways, 1999) and are expected to respond to disturbance and management actions faster than forest trees or vertebrates (Kremen et al., 1993; Oliver and Beattie, 1996a). Flightless invertebrates are also important for monitoring because these taxa do not have complex life cycles (except for ants), adults are relatively long-lived compared to other insects (Lawes et al., 2005) and they have limited ability to escape and to colonise forest patches after disturbance. These taxa generally meet Andersen’s (1999) criteria, but criteria three, five and six require further investigation.

3.1.5 *“Best practice” approaches to biodiversity assessment and monitoring*

To promote informed management specifically in the Maloti-Drakensberg Bioregion (which spans South Africa and Lesotho) and more generally in Afrotropical regions throughout Africa, recommendations for biodiversity assessment and monitoring are needed.

There is no single “best practice” to fit all circumstances. Rather these recommendations for flightless invertebrate sampling strive to evaluate the strengths and weaknesses of the various options investigated. To account for uncertainty in biodiversity measurements, minimum rather than mean estimates of richness and abundance should be

used when setting “best practice” approaches to conservation and evaluating management regimes (Taylor and Wade, 2000). This helps ensure that populations maintain “safe” levels and can recover from human-caused mortality. Management regimes can also only be evaluated in the context of specific objectives (Taylor and Wade, 2000). Here, my specific objective is the conservation of flightless invertebrate diversity in Afrotropical forest in southern Africa.

3.1.6 *Testing the “best practice” approaches*

Recommendation for season, taxa and sampling methods for monitoring invertebrates should, ideally, also be tested for verification (McGeoch, 1998; McGeoch et al., 2002). The effect of fire on the diversity of ground dwelling forest invertebrates is a useful scenario of verification of biodiversity indicator taxa and recommended sampling methods, given the management implications of protecting forests from fires. Afrotropical forests in the Drakensberg are generally found in natural fire-refugia (von Maltitz et al., 2003) and therefore forest-dependent invertebrates are likely to be fire-intolerant. In the surrounding Afrotropical grasslands, fire is widely used as a conservation management tool (Brockett et al., 2001; Parr et al., 2002) because fire is the only practical alternative for manipulating large areas of grassland vegetation. Grassland fires do occasionally penetrate Drakensberg forests (von Maltitz et al., 2003) but the effect of forest fires on ground dwelling invertebrate diversity has yet to be quantified in this system. I predict that burning will lower species richness and abundance of ground dwelling forest invertebrates, at least in the short-term.

3.1.7 *Aim and objectives*

The aim of this study was to make recommendations on which season, taxa and sampling methods are most suitable for biodiversity assessment and monitoring in the conservation of flightless invertebrates in Afrotropical forest in the KwaZulu-Natal Drakensberg, South Africa. The objectives of this study were:

- 1) To compare species richness and community structure in four different months to quantify seasonal effects on flightless invertebrates and to identify the most suitable time of year for diversity assessment and monitoring of the target taxa;
- 2) To determine which flightless invertebrate taxa are suitable for use in biodiversity assessment (surrogates) and monitoring (indicators);
- 3) To determine which sampling methods used to determine species richness are most effective and efficient for use in biodiversity assessment and monitoring for the conservation of flightless invertebrates;
- 4) To propose “best practice” recommendations for season, taxa and sampling methods for use in biodiversity assessment and monitoring; and

- 5) To test these recommendations for use in monitoring using burned and unburned Afrotropical forest patches.

3.2 MATERIALS AND METHODS

3.2.1 Study sites

Three Afrotropical forest patches (sites) were sampled to assess the effect of seasonal changes on invertebrate species richness and community structure. These forest patches were located at Injisuthi in the Maloti-Drakensberg Bioregion, KwaZulu-Natal, South Africa (Figure 3.1, Appendix 3a). Sampling took place during the months of March, June, September and December in 2004. March (autumn) and December (summer) were considered wet season months in this study, and June (winter) and September (spring) were dry season months.

The Maloti-Drakensberg Bioregion experiences summer rainfall, with 70% of the annual precipitation in summer (November to March) (Schulze, 1997). Median rainfall values in the months that seasonal sampling took place are as follows: March, 100 - 140 mm; June, < 5 mm; September, 20 - 60 mm; and December, 120 - 160 mm. Mean annual temperature in the Drakensberg is 16°C, with mean daily maximum temperatures ranging from 26.7°C in summer to 15.6°C in winter (Schulze, 1997). Temperatures can drop to below zero in winter.

The “best practice” approaches to monitoring for the impact of management actions on biodiversity were tested using eight Afrotropical forest sites at Royal Natal National Park in the Maloti-Drakensberg Bioregion, KwaZulu-Natal, South Africa (Figure 3.1). Four of the Royal Natal sites were located in an unburned valley (Thukela Gorge) and four sites in a nearby burned valley (Devil’s Hoek) (Appendix 3a). Sampling at Royal Natal took place in November 2004. The same sampling methods, sampling intensity and taxa were used as for seasonal sampling at Injisuthi.

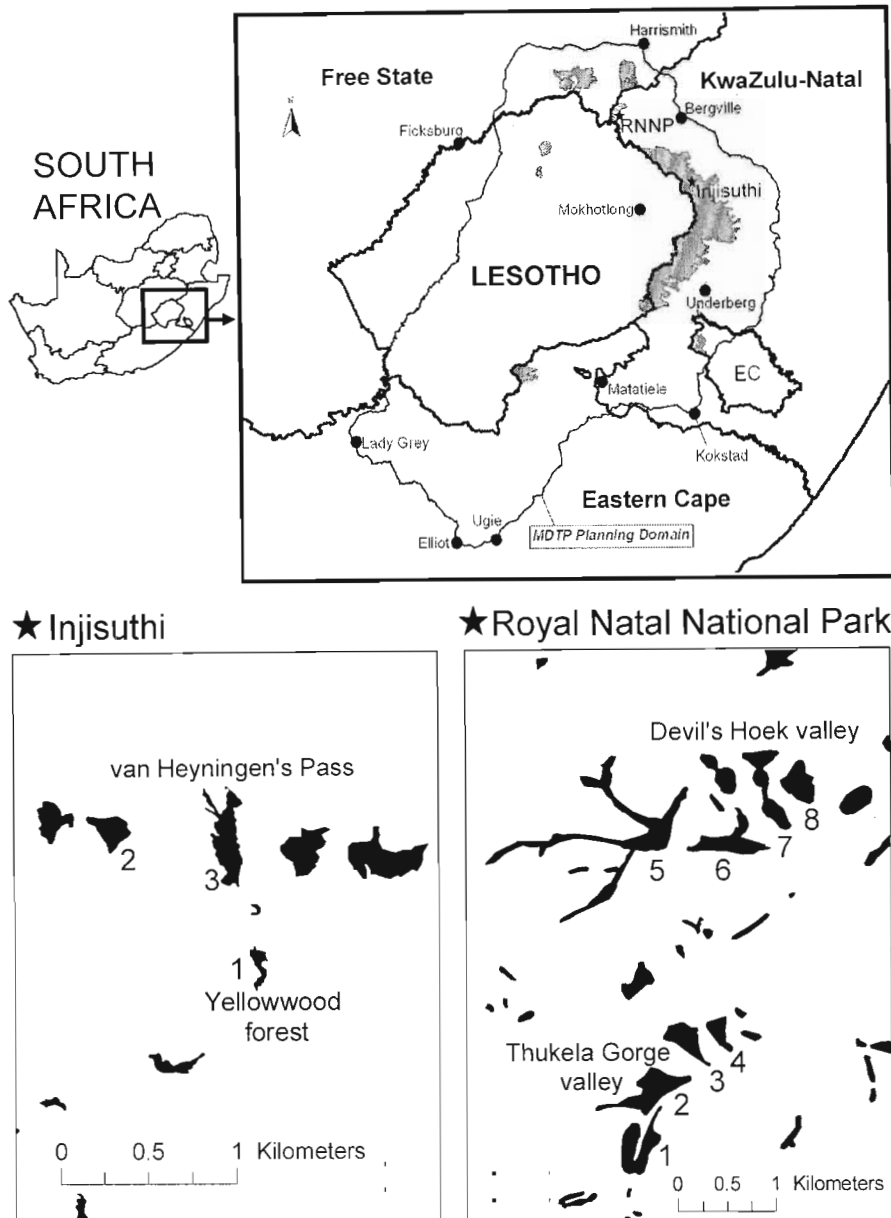


Figure 3.1. Location of Injjsuthi and Royal Natal National Park (RNNP) in the Maloti-Drakensberg Bioregion (indicated by the MDTP Planning domain) in KwaZulu-Natal, South Africa (top), with an enlargement of Injjsuthi (bottom left) showing the three forest sites and an enlargement of Royal Natal National Park (bottom right) showing the eight forest sites used to test the performance of the “best practice” approaches to monitoring. Afrotropical forest is shown in black. Site data are presented in Appendix 3a.

3.2.2 Sampling methods

Five sampling methods were used in each forest to collect flightless invertebrates. These sampling methods included soil samples, pitfall traps, leaf litter samples, active search quadrats and tree beats. Refer to Appendix 3b for tree species sampled in tree beats. Five

invertebrate target taxa were sampled: molluscs, earthworms, centipedes, millipedes and ants. Sampling methods are described in Chapter 2.2.2.

Sampling saturation

Sampling intensity was low because of time and cost constraints. Sampling was nevertheless close to saturation since field sample-based species-accumulation curves all approached an asymptote (Appendix 3c). Refer to Chapter 2.2.2 for a discussion of sampling saturation.

3.2.3 Analyses

Evaluation and comparison of the effect of season on flightless invertebrate species richness and community structure

The results from all sampling methods were combined to calculate the number of species collected from each site in each month (species richness). The total species richness of all target taxa combined and the mean species richness ($n = 3$ sites at Injisuthi) in each of the four sampling months were calculated. The number of unique species was also calculated for each sampling month. Here, unique species are those collected in one month only, regardless of which site(s) the species was found in. Rarefaction and Hill's diversity number were not used because only one site per forest was sampled. Since the number of replicates in each season was low and the same sites were sampled each month, non-parametric analyses were used. A triangular matrix of Bray-Curtis dissimilarity in the species composition between every pair of sites in every season was used to map the site inter-relationships in an ordination by non-metric multidimensional scaling (NMDS) using PRIMER (Clarke and Gorley, 2001). NMDS is often the method of choice for graphical representation of community relationships because of the flexibility and generality of its dependence only on a biologically meaningful view of the data, and its distance-preserving properties (Clarke, 1993). In an NMDS plot, the direction of maximal variation lies along the x-axis. The stress value is a reliability measure – the greater the stress, the greater the risk of drawing false inferences from an ordination. The same triangular matrix of Bray-Curtis dissimilarity between seasons was used for pairwise one-way analysis of similarity (ANOSIM) to test the null hypothesis of no difference between seasons.

Determination of suitable flightless invertebrate taxa for use in biodiversity assessment and monitoring

Data from the three Injisuthi sites were combined to calculate species richness for molluscs, centipedes, millipedes and ants in each sampling month. Earthworms and onychophorans were not analysed individually because they were not collected in all months and differences in species richness and abundance among sites and months were too low to test statistically.

NMDS ordination was performed to summarize differences in species composition of the three Injisuthi sites sampled in four different seasons for molluscs, centipedes, millipedes and ants. The same triangular matrices of Bray-Curtis dissimilarity between sites were used for pairwise one-way ANOSIM to test the null hypothesis of no difference between seasons for each of the four target taxa.

Determination of suitable sampling methods for use in biodiversity assessment and monitoring

To compare the contribution of different sampling methods to species richness counts in different seasons, the number of species collected at Injisuthi using each sampling method was calculated. Species richness from each sampling method in each month was plotted for all taxa combined and each target taxon. The number of species collected by only one sampling method in each month for all flightless invertebrate taxa combined was also plotted. This analysis was used to determine which sampling method(s) were most suitable for targeting rare species and species with short adult life cycles or short periods of surface activity. The efficiency of each sampling method (i.e. sampling effort) was calculated as the total number of species recorded in three forests combined, divided by the number of person hours required for sampling and processing. Efficiency (species per person hour) was calculated for each sampling method in each month. Mean efficiency for each sampling method was calculated as the mean of four months.

Determination of the “best practice” approaches for season, taxa and sampling methods for use in biodiversity assessment and monitoring

Data on flightless invertebrate taxa collected during seasonal sampling in Afrotropical forest at Injisuthi were used to construct a summary table of the “best practice” approaches to (a) biodiversity assessment and (b) monitoring for the impact of management actions. This summary was based on criteria for recommended season, taxa and sampling methods.

Test of proposed “best practice” approaches using burned and unburned Afrotropical forest sites

To test the “best practice” approaches to monitoring, total mollusc species richness and mean species richness were compared between unburned and burned valleys at Royal Natal National Park using analysis of variance (ANOVA). According to Ezemvelo KZN Wildlife fire records, Devil’s Hoek valley was last burned in 2003, while Thukela Gorge forests have not been burned during the same time period. Mollusc species richness measured by quadrat, litter sample and tree beat sampling was compared to determine methods required to sample mollusc species richness for monitoring purposes. The species richness of live molluscs was

compared to the species richness of mollusc shells to determine whether shells alone could be used for monitoring. To determine whether mollusc species richness reflected the influence of fire on the species richness of other flightless invertebrates, total and mean species richness were calculated for the unburned and burned valleys. Mollusc data were also compared with centipede, millipede and ant data.

3.3 RESULTS

A total of 4275 individual specimens representing 55 morphospecies were collected in the four months from the three sites at Injisuthi (Appendix 3d). The 55 morphospecies comprised 26 mollusc, four earthworm, one onychophoran, six centipede, 11 millipede and seven ant species. Of these 55 species, 22 were recorded in all four months, 11 in three of the four months, seven in two of the four months and eleven species were collected in one month only (Appendix 3d).

3.3.1 *Evaluation and comparison of the effect of season on flightless invertebrate species richness and community structure*

Total species richness, mean species richness \pm one standard deviation and unique species richness for all taxa showed a similar trend of lower richness in June and September (dry season months) compared to March and December (wet season months) (Figure 3.2a). No species were unique to winter dry season months (Figure 3.2a). This suggests that the flightless invertebrate community in winter is merely a subset of the summer wet season community. Therefore, winter dry season sampling for biodiversity assessments and/or monitoring is not necessary.

This pattern was confirmed by the NMDS ordination, in which sites were primarily separated across the x-axis according to wet and dry season months (Figure 3.2b). Sites were secondarily clustered according to month, with December separated from March samples, and September from June samples across the y-axis (Figure 3.2b). Thus flightless invertebrate species composition was distinctly different between the wet and dry season, but also differed within seasons.

Pairwise tests for one-way ANOSIM comparing species composition between months showed that seasonal species turnover did take place. Significant differences in species composition occurred between March and June ($R = 0.852$), March and September ($R = 0.815$), March and December ($R = 0.778$), June and December ($R = 0.778$), and September and December ($R = 0.963$). However, species composition between the two dry season months, June and September, was not significantly different ($R = 0.278$).

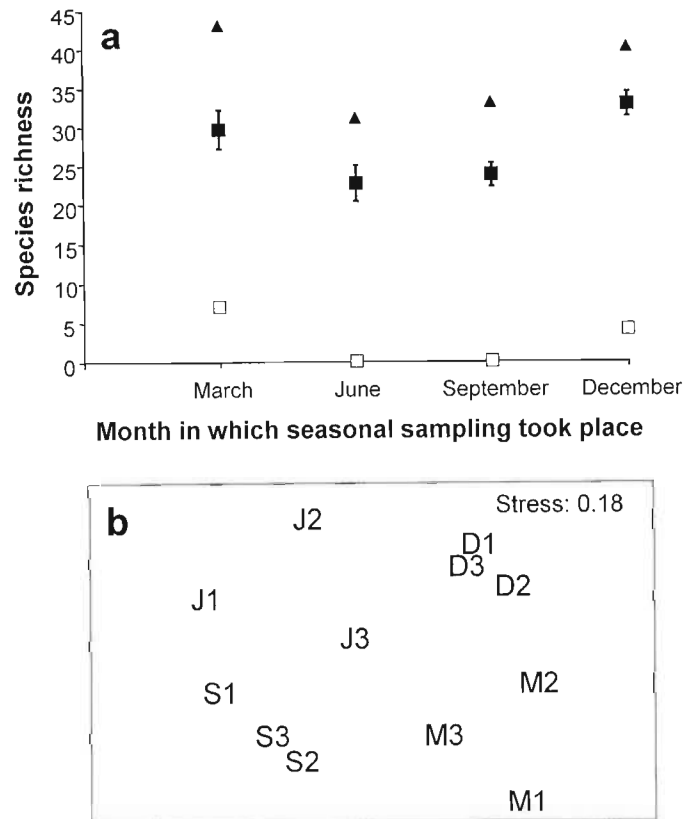


Figure 3.2. The influence of season on (a) total species richness (▲), mean species richness \pm one standard deviation (■) and unique species (□) and (b) a two-dimensional ordination from non-metric multidimensional (NMDS) scaling, applied to a triangular dissimilarity matrix of species composition for flightless invertebrates in Afrotemperate forest. M = March, J = June, S = September and D = December.

3.3.2 Determination of suitable flightless invertebrate taxa for use in biodiversity assessment and monitoring

Species richness counts of molluscs, centipedes, and millipedes were slightly higher in wet season months (March and December) than dry season months (Figure 3.3). Mollusc species composition differed between the wet and dry season months, but also within the wet season, with March samples clustering separate from December samples (Figure 3.4a). Centipede species composition also differed between the wet and dry seasons and within the wet season (Figure 3.4b). Centipede species composition within the dry season may have been more strongly influenced by site location than sampling month, but since no centipedes were collected in September from two sites this result was difficult to confirm. Millipede species composition differed among months, but separation between March and June samples was not evident (Figure 3.4c). There was also no clear separation between wet and dry season months for millipedes. Ant species composition does not appear to be strongly

influenced by season since there was no clear separation of sites according to month or wet and dry season (Figure 3.4d).

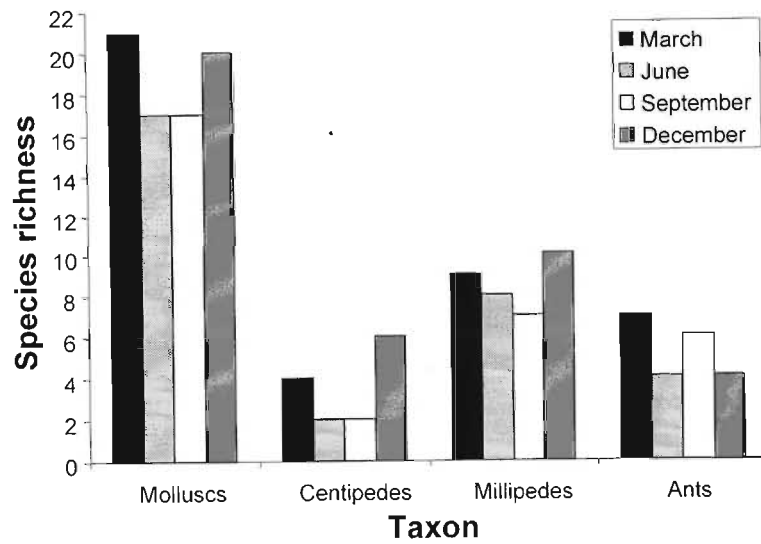


Figure 3.3. The influence of season on the species richness of individual flightless invertebrate taxa to determine their suitability for use in biodiversity assessment and monitoring for flightless invertebrate conservation.

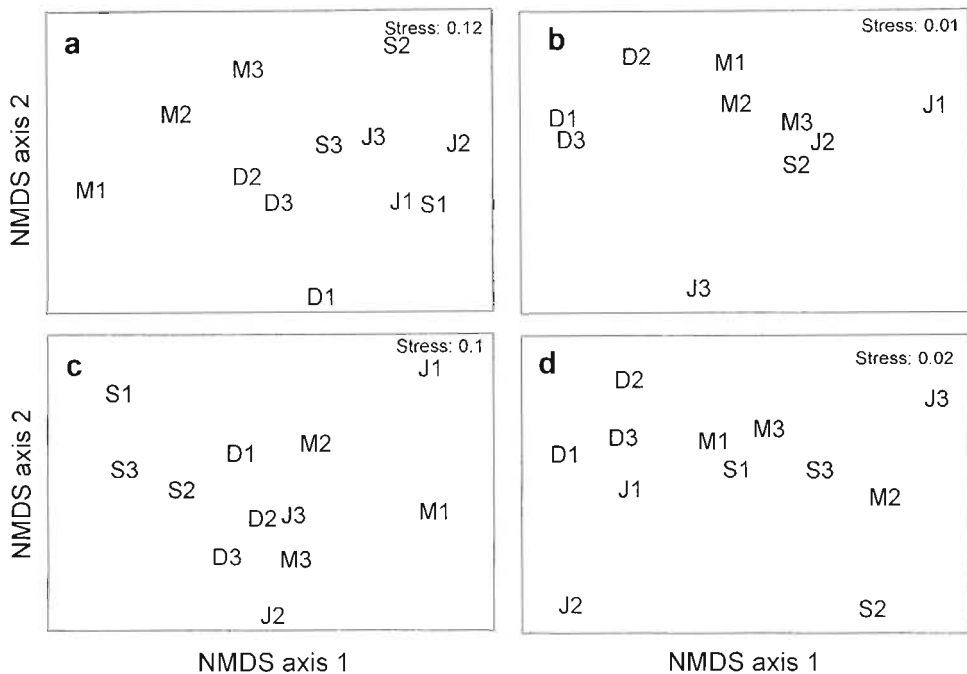


Figure 3.4. Non-metric multidimensional scaling (NMDS) ordination showing the difference in species composition of three Injisuthi sites sampled in four different seasons for (a) molluscs, (b) centipedes, (c) millipedes and (d) ants. M = March, J = June, S = September and D = December.

Individual target taxa differed in their relative similarity in species composition between sites (Table 3.1). ANOSIM for mollusc species composition showed that the greatest dissimilarity between pairs of months (i.e. the greatest temporal turnover) was between months separated by wet and dry seasons. There was significant temporal turnover in mollusc species composition between March and June ($R = 0.889$), March and September ($R = 0.796$), and June and December ($R = 0.944$). There was overlap between mollusc species composition in March and December ($R = 0.519$), suggesting some temporal turnover within the wet season. Mollusc species composition was similar between the two dry season months, June and September ($R = -0.074$) suggesting that temporal turnover does not take place within the dry season. Centipedes showed distinct temporal turnover in species composition within the wet season (March and December, $R = 0.889$). ANOSIM showed separation in centipede species composition between September and December ($R = 1.000$) and June and September ($R = -0.556$). No centipedes were collected from two sites in September, thus explaining this large temporal turnover. For millipedes, the only strong separation between pairs of months was between September and December ($R = 0.907$). Although not as clear, there was temporal turnover in millipede species composition between March and September ($R = 0.667$) and June and September ($R = 0.556$). Ant species composition was strongly separated between September and December ($R = 0.796$), but temporal turnover was also evident between March and December ($R = 0.685$).

None of the invertebrate taxa investigated in this study fit Pearson's (1994) first criterion for surrogates for biodiversity assessment, namely that the surrogate is not strongly seasonal. Therefore, flightless invertebrate surrogate and indicator taxa should be chosen based on the other criteria set by Pearson (1994) and Andersen (1999).

Table 3.1. Pairwise tests for one-way ANOSIM comparing species richness of individual taxa between months to show seasonal species turnover. R is a relative measure of separation between months.

Months		Molluscs		Centipedes		Millipedes		Ants	
		R	P	R	P	R	P	R	P
March	June	0.889	0.10	0.185	0.40	-0.389	1.00	0.167	0.40
March	September	0.796	0.10	-0.111	0.75	0.667	0.10	-0.259	1.00
March	December	0.519	0.60	0.889	0.10	0.247	0.20	0.685	0.10
June	September	-0.074	0.10	-0.556	1.00	0.556	0.10	0.204	0.30
June	December	0.944	0.10	0.704	0.10	0.111	0.20	0.241	0.20
September	December	0.648	0.10	1.000	0.25	0.907	0.10	0.796	0.10

3.3.3 Determination of suitable sampling methods for use in biodiversity assessment and monitoring

In general, the relative contribution to species richness counts of each sampling method was roughly constant across the four months in which sampling took place (Figure 3.5). However, the five different sampling methods used contributed unequally to the species richness counts of flightless invertebrates (Figure 3.5). Active search quadrats and leaf litter samples were the only sampling methods that targeted all taxa, and made the greatest contribution to species richness counts for most taxa. Tree beats were important for collecting live snails and ants, but did not target any other taxa. Pitfall traps and soil samples performed poorly and consequently are not suitable methods for use in biodiversity assessment or monitoring.

Active search quadrats and leaf litter samples were the sampling methods that collected the greatest number of species collected by one method only in each month (Figure 3.6) and far outperformed the other three sampling methods in terms of number of species collected.

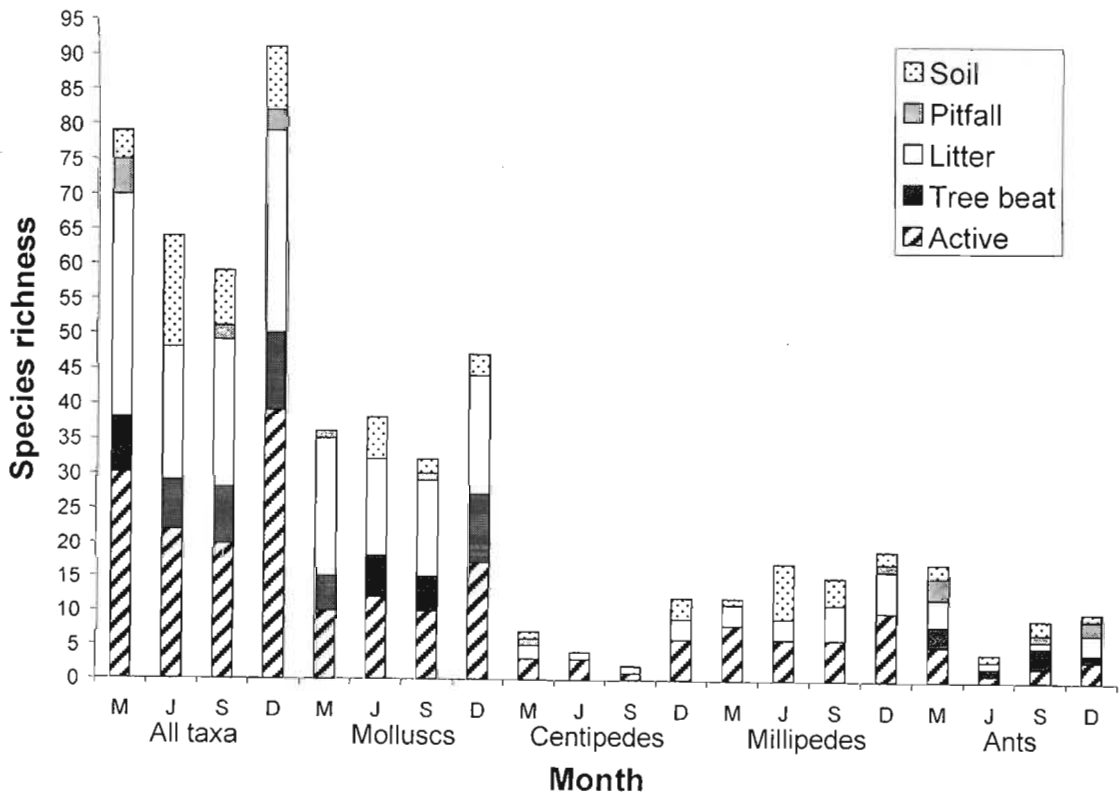


Figure 3.5. The contribution of different sampling methods to species richness counts ($n = 3$ forests) for all taxa and individual taxa in different seasons to determine the most suitable sampling method(s) for use in biodiversity assessment and monitoring for flightless invertebrate conservation. M = March, J = June, S = September and D = December.

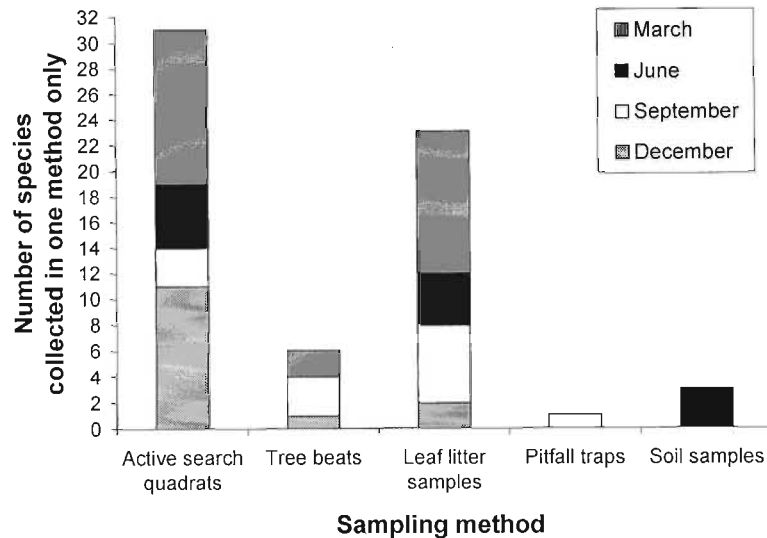


Figure 3.6. The number of species unique to one sampling method in each season (month) to determine the most suitable sampling method(s) for use in biodiversity assessment and monitoring for flightless invertebrate conservation.

The time taken for each activity and calculations of efficiency for each sampling method are presented in Appendix 3e. The mean efficiency of each sampling method is summarized in Table 3.2. Leaf litter samples and active search quadrats were the most efficient sampling methods because they yielded the highest number of species per person hour (Table 3.2).

Table 3.2. Mean efficiency of each sampling method to evaluate the suitability of different sampling methods for use in biodiversity assessment and monitoring.

Sampling method	Mean efficiency (spp./person hour)
Soil samples	1.0
Pitfall traps	0.2
Litter samples	2.6
Quadrats	2.6
Tree beats	1.4

3.3.4 Determination of the “best practice” approaches for season, taxa and sampling methods for use in biodiversity assessment and monitoring

Criteria for biodiversity assessment and monitoring were identified for season, taxa and sampling methods from data collected at Injisuthi. Using these criteria, “best practice” approaches to invertebrate biodiversity assessment and monitoring for the impact of management actions on invertebrate biodiversity were summarized (Table 3.3).

Table 3.3. “Best practice” approaches to biodiversity assessment and monitoring for the impact of management actions on biodiversity based on seasonal sampling of flightless invertebrates in Afrotropical forest at Injisuthi in the KwaZulu-Natal Drakensberg.

	Criteria for biodiversity assessment	Biodiversity assessment	Criteria for monitoring	Monitoring
Best season	The season in which the highest species richness of target taxa was measured, on condition unique assemblages are not found in different seasons.	Wet season (December to March)	The season in which the highest species richness of target taxa was measured.	Wet season (December to March)
Best taxa	Taxa that (1) have relatively high species richness and abundance; (2) include both rare and common species; (3) show high levels of endemism at the local scale; (4) have a well known and stable taxonomy; (5) are easy to find and identify; and (6) represent other invertebrate taxa (Pearson, 1994).	Molluscs Millipedes	Six criteria should be considered when choosing indicator taxa for monitoring: (1) their distribution and diversity should be relatively well known; (2) they must be functionally important in ecosystems; (3) they must show sensitivity to environmental change; (4) be easily sampled, sorted and identified; (5) their response to environmental change must be reliably interpreted; and (6) they must accurately reflect the responses of other taxa (Andersen, 1999).	Molluscs
Best sampling methods	The method(s) that samples the highest number of species, including rare and threatened species.	Active search quadrats and litter samples	Consistent across seasons, sample species richness, and have a feasible time required for sampling and processing.	Active search quadrats and litter samples, but tree beats should be included to collect live snails.

3.3.5 Test of proposed “best practice” approaches for monitoring using burned and unburned Afrotemperate forest sites

Since molluscs met Andersen’s (1999) criteria, their ability to reflect disturbance and the reaction of other taxa was tested. Mollusc species collected using active search quadrats; leaf litter samples and tree beats from Royal Natal National Park were used for this test (Appendix 3f). Forest sites in two valleys at Royal Natal were compared: Thukela Gorge valley (unburned) and Devil’s Hoek valley (burned).

Molluscs responded negatively to burning. The total species richness and mean species richness ± 1 SD for molluscs was lower in burned than unburned sites for (1) active search quadrats and litter samples, (2) active search quadrats, litter samples and tree beats, (3) shells only and (4) live snails only (Figure 3.7a and b). The species richness was significantly different between burned and unburned sites using shells only ($F_{2,6} = 3.411$, $P = 0.038$). A response to disturbance can therefore be detected using snail shells only. Therefore, using the sampling method of tree beats to collect live snails is not necessary when monitoring the impacts of fire on flightless invertebrates.

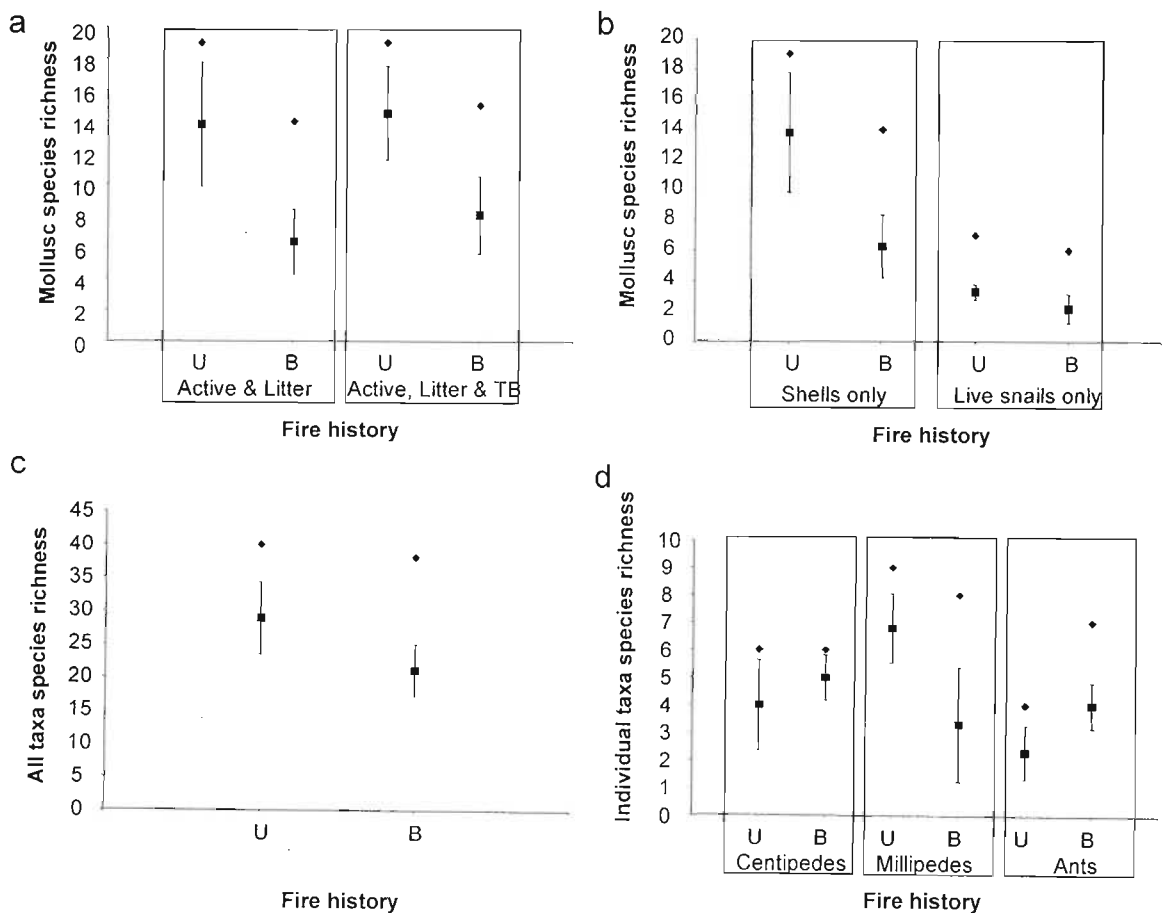


Figure 3.7. Test of the “best practice” approaches to monitoring using the influence of fire history on the total species richness (◆) and mean species richness \pm one standard deviation (■) of (a) molluscs with and without tree beats, (b) molluscs using shells only and live snails

only, (c) all taxa and (d) individual taxa. U = unburned ($n = 4$ forest sites) and B = burned ($n = 4$ forest sites). Active = active search quadrats, litter = leaf litter samples and TB = tree beats.

The pattern of response to fire history of molluscs mirrored that of all target taxa combined (Figure 3.7c). Molluscs are therefore a suitable indicator of disturbance for flightless invertebrate diversity in general. However, individual taxa varied in their response to fire history (Figure 3.7d). Millipedes, like molluscs, had lower species richness in burned than unburned sites. Ants, however, had higher species richness in burned sites than unburned sites. Centipedes showed little difference between unburned and burned sites, and so do not show a response to burning 18 months post-burn. Thus three of the four taxa investigated responded to fire, some negatively (molluscs and millipedes), others positively (ants). So long as a response to disturbance is detected, the direction need not always be the same. The “best practice” approach satisfied predictions and therefore performed well in response to the effect of burning on forest dwelling invertebrate species richness.

In general, the abundance of molluscs was higher in Thukela Gorge valley than Devil's Hoek valley (Appendix 3f). Three species (*Trachycystis contabulata*, *T. ectima* and *Sheldonia transvaalensis*) had higher abundance in Devil's Hoek valley than Thukela Gorge valley.

3.4 DISCUSSION

3.4.1 Seasonal changes in species richness and community composition

Season is an important consideration for biodiversity monitoring because it has a relatively short-term temporal effect on diversity. Plant architecture and phenology change seasonally (Curry, 1994), which directly and indirectly influence invertebrates. Although relatively long-lived, molluscs, earthworms, onychophorans, centipedes and millipedes are sensitive to desiccation and are inactive during the dry season (Lawrence, 1984; Curry, 1994; Hamer et al., 1997; Herbert and Kilburn, 2004). Taxa such as molluscs bury themselves deep in the soil at the base of trees and shrubs, among dense clumps of plants or under logs, where they remain dormant until late spring when the rains begin (Herbert and Kilburn, 2004). Ant species richness is also significantly lower in winter than at other times of year (Kotze, 2000; Leponce et al., 2004). Invertebrates are generally more abundant and species rich in Afrotropical forests during the wet season than the dry season months, but patterns of inter-seasonal diversity for amphipods, carabids and ants in an Afrotropical forest in the KwaZulu-Natal midlands are consistent (Kotze, 2000). The results of this study are consistent with Kotze's (2000) findings.

The flightless invertebrate community structure might also reflect temperature change or frost occurrence. In this study, sub-zero minimum temperatures and frost were recorded on all sampling days during both June and September. The average daily minimum

temperature in winter in the Drakensberg is -1.1°C and frost is common (Schulze, 1997). Sampling for assessments or monitoring therefore should not take place in the winter months, even though it appears that many flightless, ground dwelling invertebrates do not show the same short-term turnover as would be expected for insects in general. Many flies, butterflies and beetles for example, are present in the adult, identifiable and active stage for a matter of days or a few weeks (Scholtz and Holm, 1985), so for such taxa, spatial and inter-annual comparisons would have to be carried out within the same month.

3.4.2 *Surrogates for flightless invertebrate diversity in Afrotropical forests*

Biodiversity assessment is a widely used tool for biodiversity conservation in many different habitats. In terrestrial environments plants, birds and butterflies are commonly used, are usually the only taxa sampled, and other invertebrates are often overlooked (New, 1998; Grove and Stork, 1999). Research has, however, shown that vegetation types cannot always be used as surrogates for invertebrates (Howard et al., 1998; York, 1999), and that levels of endemism and diversity of invertebrates are much higher than those for trees and vertebrates (Ponder, 1999). Their importance in terms of ecosystem functioning (Heywood and Baste, 1995) and their diversity (Colwell and Coddington, 1994) necessitates the development of protocols for including at least some invertebrate taxa in such programmes.

At a species level, the onychophoran *Opisthopatus cinctipes* and the carnivorous slug *Chlamydephorus burnupi* would be useful for inclusion in assessments purely to include a rare and endemic species respectively.

Congruency across taxa in terms of species richness requires further investigation, but most other studies on this topic have only found weak relationships between richness of different taxa (Prendergast et al., 1993; Lombard, 1995; Howard et al., 1998; Lawton et al., 1998; Kotze and Samways, 1999; Kati et al., 2004). Millipedes and molluscs are potentially suitable surrogates for biodiversity assessment because they do meet the other criteria specified by Pearson (1994) for biodiversity surrogates. The number of species sampled meant that identifications were manageable, and that adequate diversity was measured to allow comparisons.

3.4.3 *Indicators for flightless invertebrate diversity in Afrotropical forests*

Onychophorans are not represented by sufficient diversity or abundance to allow their use in comparative monitoring in Drakensberg forests and this may also be the case for earthworms and centipedes. Nevertheless, monitoring of populations may be required and species such as *O. cinctipes* and *C. burnupi* should not be collected, but recorded and released immediately on site to prevent unnecessary negative impacts on their populations.

Ants are probably the most commonly used invertebrate indicator taxon in terrestrial ecosystems in Australia (New, 2000; Andersen et al., 2004) and their robustness as

ecological indicators has been consistently demonstrated (Andersen and Majer, 2004). While ants may potentially be useful indicators of disturbance such as fire in South African savannas (Parr et al., 2002), their suitability as indicators in Afrotropical forest in the Drakensberg is questionable since they are not suitable surrogates for biodiversity assessment. Ants had low species richness in all months, and very little turnover between months. Ants also did not show a similar response to fire compared to other taxa investigated.

The terrestrial amphipod, *Talitriator africana*, and staphylinid beetles have been suggested as possible indicators of disturbance in Afrotropical forest (Lawes et al., 2005). Amphipods are, however, not present in all forests in the Drakensberg and no amphipods were collected in any of the forests sampled at either Injisuthi or Royal Natal National Park. It is not known whether the absence of amphipods in Drakensberg forests is a result of disturbance, since the history of these forests is likely, in most cases, to be similar.

3.4.4 Sampling methods

In terms of the sampling methods used in this study, soil samples and pitfall traps performed poorly. In addition, soil samples are heavy to carry in the field and require Berlese funnels which are not available to most managers or conservation practitioners in the field. The performance of pitfall trapping could probably be improved by leaving traps out for longer in the field (Borgelt and New, 2006). Tree beating of sub-canopy branches was an effective means of collecting live material of snails, as well as a different suite of ants compared to that found on the soil surface or in leaf litter. Tree beating would only be necessary for biodiversity assessments, since it did not have any impact on the trend identified for molluscs in burned and unburned forests. Litter samples are critical for sampling micro-molluscs, and they also provide species that may be missed during active sampling. Active searching using marked quadrats should still complement leaf litter sampling because active searching can cover a wider area and variety of microhabitats (such as under rocks) that would be missed in leaf litter samples. Druce et al. (2004) similarly found that active searching of quadrats was the most effective means of sampling millipedes and centipedes in South African savanna. Active searching is likely to yield longer species lists, makes far more efficient use of time and requires smaller quantities of consumable items, such as ethanol, than pitfall trapping (Mesibov et al., 1995). Duplicate specimens and non-target taxa can easily be released using this method, which means that it has less impact on the fauna than destructive sampling such as pitfall traps. This is important to consider for long term monitoring programmes.

Post-mortem sampling of molluscs is reliable because most species can be identified based on their shell characteristics (Herbert and Kilburn, 2004). Post-mortem sampling has several advantages: (1) biodiversity assessment and monitoring can take place in any

season, (2) species richness estimates are less dependent on weather conditions during sampling, (3) collecting shells has a lower impact on the mollusc community than removing live individuals, and (4) shells provide higher abundance estimates than relying on live individuals alone. High abundance affords statistical rigor in data analysis (Kremen et al., 1993). Those species that reacted particularly strongly to fire could be the focus of monitoring programmes. However, two important questions remain unanswered and require further research. Firstly it is unknown what happens to dead, empty shells during a fire and micro-mollusc shells are unlikely to survive ground fires because they are thin and delicate. Secondly the possibility exists that post-fire conditions may result in many mollusc individuals dying, thereby increasing the number of shells in the litter post-fire.

3.4.5 Conclusion

Effective protocols for assessment and monitoring are likely to be habitat specific, and the suggestions presented here will probably only be applicable to Afrotropical forest. However, even in protected areas these habitats may be under threat from runaway fires, alien invasive plants and increasing levels of human disturbance through ecotourism or harvesting of certain plants.

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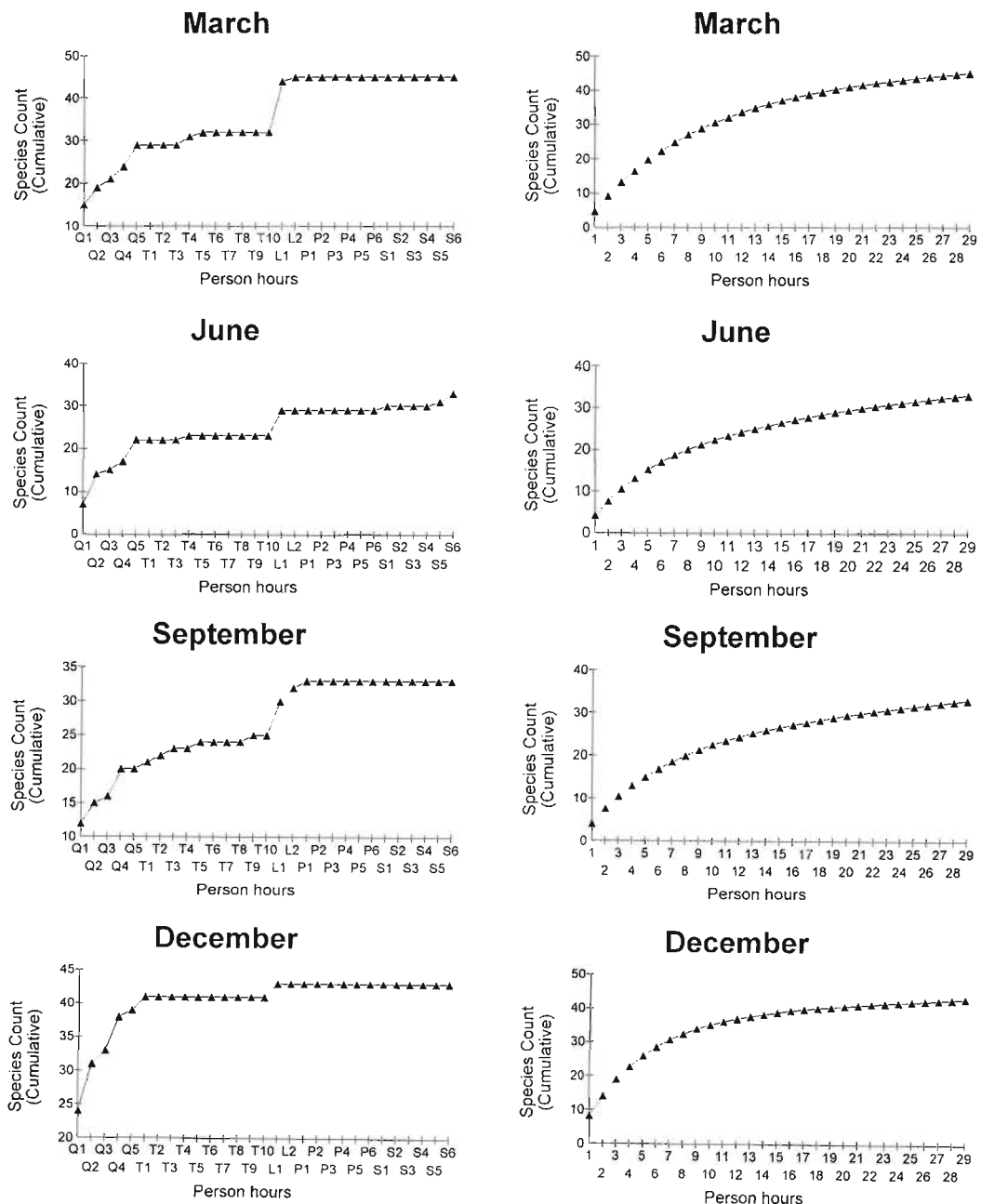
Appendix 3a. Location, area, altitude and mean annual precipitation (MAP) of the three forest patches sampled at Injisuthi and the eight forest patches at Royal Natal National Park (RNNP) used to test the performance of the “best practice” approaches to monitoring.

Reserve	Site	Valley	Co-ordinates		Area (ha)	Altitude (m a.s.l.)	MAP (mm)
			(GSW 84)				
Injisuthi	1	Yellowwood	29.1197 S	29.4359 E	1.41	1500	1022
Injisuthi	2	Van Heyningen's Pass	29.1079 S	29.4334 E	2.46	1650	1076
Injisuthi	3	Van Heyningen's Pass	29.1100 S	29.4389 E	5.28	1600	1022
RNNP	1	Thukela Gorge	28.7316 S	28.9134 E	12.50	1700	1327
RNNP	2	Thukela Gorge	28.7305 S	28.9180 E	14.00	1600	1327
RNNP	3	Thukela Gorge	28.7292 S	28.9212 E	7.64	1620	1327
RNNP	4	Thukela Gorge	28.7276 S	28.9237 E	4.26	1600	1327
RNNP	5	Devil's Hoek	28.7102 S	28.9182 E	35.70	1700	1225
RNNP	6	Devil's Hoek	28.7105 S	28.9244 E	12.00	1620	1225
RNNP	7	Devil's Hoek	28.7089 S	28.9287 E	11.40	1620	1142
RNNP	8	Devil's Hoek	28.7111 S	28.9313 E	8.28	1550	1142

Appendix 3b. Checklist of tree species sampled in tree beats. Trees were identified in the field using Pooley (2003).

Family	Genus	species	Authority	English common name	Site
Apocynaceae	<i>Carissa</i>	<i>bispinosa</i>	(L.) Desf. Ex Brenan	Forest Num-num	1,2,3
Aquifoliaceae	<i>Ilex</i>	<i>mitis</i>	(L.) Radlk.	Cape Holly	1
Balanitaceae	<i>Clausena</i>	<i>anisata</i>	(Wild.) Hook.f. ex Benth.	Horsewood	1,2
Celastraceae	<i>Maytenus</i>	<i>undata</i>	(Thunb.) Blakelock	Koko Tree, South African Holly	2
Ebenaceae	<i>Diospyros</i>	<i>whyteana</i>	(Hiern) F. White	Bladder-nut, Blackbark	1,2
Ebenaceae	<i>Euclea</i>	<i>crispa</i>	(Thunb.) Guerke	Blue Guarri	1
Flacourtiaceae	<i>Trimeria</i>	<i>grandifolia</i>	(Hochst.) Warb.	Wild Mulberry	1,2,3
Icacinaceae	<i>Cassinopsis</i>	<i>ilicifolia</i>	(Hochst.) Kuntze	Lemon Thorn	2
Lauraceae	<i>Cryptocarya</i>	<i>woodii</i>	Engl.	Cape Quince, Bastard Camphor Tree	1,2
Oliniaceae	<i>Olinia</i>	<i>emarginata</i>	Burr Davy	Mountain Hard Pear	3
Podocarpaceae	<i>Podocarpus</i>	<i>henkelii</i>	Stapf ex Dallim. Jacq.	Henkel's Yellowwood	1
Podocarpaceae	<i>Podocarpus</i>	<i>latifolius</i>	(Thunb.) R.Br. Ex Mirb.	Real Yellowwood	1,2,3
Rubiaceae	<i>Canthium</i>	<i>ciliatum</i>	(Klotzsch) Kuntze	Hairy Turkey-berry, Dwarf Turkey-berry	2

Appendix 3c. *Sample-based field species-accumulation curves (left) and randomized species-accumulation curves (right) of all target taxa combined in each month that seasonal sampling took place. The x-axes represent the number of person hours taken to collect and process each sampling replicate. Q = one 2 x 2 m active search quadrat, T = five tree beats from one tree, L = one 2 l leaf litter sample, P = one 125 ml pitfall trap, and S = one 300 ml soil sample. RG = Rugged Glen Nature Reserve, RN = Royal Natal National Park, CP = Cathedral Peak and IN = Injisuthi. The numbers represent sites sampled within each reserve.*



Appendix 3d. List of the mollusc, earthworm, onychophoran, centipede, millipede and ant species collected during seasonal sampling at Injisuthi, within the Maloti-Drakensberg Bioregion, KwaZulu-Natal, South Africa, with abundance data for M = March, J = June, S = September and D = December.

Sp.	Order	Family	Genus	species	Authority	M	J	S	D
Class Gastropoda									
1	Neeritopsina	Hydrocenidae	<i>Hydrocena</i>	<i>noticola</i>	Benson, 1856	169	168	334	169
2	Architaenioglossa	Cyclophoridae	<i>Chondrocyclus</i>	<i>isipingoensis</i>	(Sturany, 1898)	25	54	29	34
3	Eupulmonata	Pupillidae	<i>Lauria</i>	<i>dadion</i>	(Benson, 1864)	12	9	5	7
4	Eupulmonata	Orculidae	<i>Fauxulus</i>	<i>glanvilleanus (darglensis)</i>	(Ancey, 1888)	23	36	88	50
5	Eupulmonata	Orculidae	<i>Fauxulus</i>	<i>mcbearianus</i>	Melville and Ponsonby, 1901	15	17	25	56
6	Eupulmonata	Orculidae	<i>Fauxulus</i>	sp.		5	0	0	0
7	Eupulmonata	Vertiginidae	<i>Pupisoma</i>	<i>harpula</i>	(Reinhardt, 1886)	5	0	0	14
8	Eupulmonata	Vertiginidae	<i>Truncatellina</i>	<i>sykesii</i>	(Melville and Ponsonby, 1893)	60	50	67	35
9	Eupulmonata	Clausiliidae	<i>Macroptychia</i>	<i>africana</i>	(Melville and Ponsonby, 1899)	15	12	13	13
10	Eupulmonata	Achatinidae	<i>Archacatina</i>	sp.		0	0	0	13
12	Eupulmonata	Streptaxidae	<i>Gulella</i>	<i>mariae</i>	(Melville and Ponsonby, 1892)	10	12	8	9
16	Eupulmonata	Valloniidae	<i>Acanthinula</i>	sp.		35	0	1	24
17	Eupulmonata	Charopidae	<i>Afrodonta</i>	<i>novemlamellaris</i>	(Burnup, 1912)	10	11	0	6
18	Eupulmonata	Charopidae	<i>Trachycystis</i>	<i>contabulata</i>	Connolly, 1932	11	65	46	33
19	Eupulmonata	Charopidae	<i>Trachycystis</i>	<i>ectima</i>	(Melville and Ponsonby, 1899)	0	13	14	25
20	Eupulmonata	Charopidae	<i>Trachycystis</i>	<i>rudicostata</i>	Connolly, 1923	94	91	51	31
21	Eupulmonata	Charopidae	<i>Trachycystis</i>	<i>subpinguis</i>	Connolly, 1922	0	0	0	14
22	Eupulmonata	Charopidae	<i>Trachycystis</i>	<i>glanvilliana</i>	(Ancey, 1893)	0	2	3	1
23	Eupulmonata	Charopidae	<i>Trachycystis</i>	<i>venatorum</i>	Connolly, 1932	23	0	0	0
24	Eupulmonata	Helicarionidae	<i>Kaliella</i>	<i>euconuloides</i>	Melville and Ponsonby, 1908	26	8	29	117
25	Eupulmonata	Euconulidae	<i>Afroconulus</i>	<i>diaphanus</i>	(Connolly, 1922)	10	5	7	4
27	Eupulmonata	Achatinidae	<i>Archacatina</i>	<i>dimidiata</i>	(Smith, 1878)	0	2	1	1
28	Eupulmonata	Vertiginidae	<i>Pupisoma</i>	<i>orcula</i>	(Benson, 1850)	14	63	86	0
29	Eupulmonata	Pupillidae	? <i>Pupilla</i>	<i>fontana</i>	(Krauss, 1848)	3	0	0	0
30	Eupulmonata	Charopidae	<i>Trachycystis</i>	sp.		1	0	0	0
264	Eupulmonata	Chlamydephoridae	<i>Chlamydephorus</i>	<i>burnupi</i>	Smith, 1892	2	0	0	0
Class Oligochaeta									
254	Haplotaxida	Acanthodrilidae	<i>Dichogaster</i>	sp.		0	0	0	4
255	Haplotaxida	Acanthodrilidae	<i>Parachilota</i>	sp. 1		0	0	0	29
256	Haplotaxida	Acanthodrilidae	<i>Parachilota</i>	sp. 2		3	0	0	1
262	Opisthophora	Microchaetidae	<i>Proandricus</i>	sp.		0	0	0	3
Class Onychophora									
263	Onychophora	Onychophora	<i>Opisthopatus</i>	<i>cinctipes</i>	Purcell, 1899	1	0	0	0
Class Chilopoda									
45	Geophilomorpha	Geophilidae	<i>Rhysida</i>	<i>afra (afra)</i>		0	0	0	11
47	Geophilomorpha	Geophilidae		sp. 2		0	0	0	36
48	Geophilomorpha	Geophilidae		sp. 1		8	7	1	20
49	Lithobiomorpha	Henicopidae	<i>Paralamyctes</i>	<i>spenceri</i>		4	5	3	1
50	Lithobiomorpha	Henicopidae	<i>Lamyctes</i>	<i>africana</i>		2	0	0	92
51	Lithobiomorpha	Henicopidae	<i>Lamyctes</i>	sp.		3	0	0	1
Class Diplopoda									
32	Sphaerotheriida	Sphaerotheriidae	<i>Sphaerotherium</i>	<i>perbrincki</i>	Schubart, 1958	0	0	0	0
33	Sphaerotheriida	Sphaerotheriidae	<i>Sphaerotherium</i>	<i>dorsale</i>	(Gervais, 1847)	2	3	63	23
34	Sphaerotheriida	Sphaerotheriidae	<i>Sphaerotherium</i>	<i>mahaum</i>	Schubart, 1958	75	27	26	180
35	Sphaerotheriida	Sphaerotheriidae	<i>Sphaerotherium</i>	sp.		0	0	12	19
36	Polydesmida	Dalodesmidae	<i>Gnomeskelus</i>	sp.		27	5	7	74
37	Polydesmida	Gomphodesmidae	<i>Ulodesmus</i>	<i>simplex</i>	Lawrence, 1953	4	7	18	32
38	Polydesmida	Gomphodesmidae	<i>Gnomeskelus</i>	<i>montivagus</i>	Verhoeff, 1939	1	6	2	27
39	Polydesmida	Gomphodesmidae	<i>Gnomeskelus</i>	<i>attemsii</i>	Verhoeff, 1939	1	1	0	23
40	Spirostreptida	Odontopygidae	<i>Spinotarsus</i>	sp. 2		1	0	16	1
41	Spirostreptida	Odontopygidae	<i>Spinotarsus</i>	sp. 1		1	1	0	3
43	Spirostreptida	Spirostreptidae	<i>Doratogonus</i>	<i>montanus</i>	Hamer, 2000	0	0	0	0
Class Insecta									
53	Hymenoptera	Formicidae		sp. 1		3	0	1	0
54	Hymenoptera	Formicidae		sp. 2		9	0	2	520
55	Hymenoptera	Formicidae		sp. 3		20	0	18	18
56	Hymenoptera	Formicidae		sp. 4		5	0	0	6
57	Hymenoptera	Formicidae		sp. 5		7	12	17	16
58	Hymenoptera	Formicidae		sp. 6		8	1	14	0
59	Hymenoptera	Formicidae		sp. 7		16	1	4	0

Appendix 3e. Efficiency of sampling methods, calculated as the number of species recorded in three forests divided by the number of person hours required for sampling and processing. M = March, J = June, S = September and D = December.

Activity	Time per forest (minutes)	Time for 3 forests (minutes)	Time for 3 forests (hours)	Species richness (n = 3 forests)				Efficiency (spp. /person hour)						
				M	J	S	D	M	J	S	D	Mean		
Lay tape measure and dig samples	30													
Set up Berlese funnels	30													
Processing	120													
<i>Soil TOTAL</i>	180	540	9	4	15	8	9	0.4	1.7	0.9	1.0	1.0		
Lay tape measure and set traps	20													
Collect traps	10													
Processing	180													
<i>Pitfall TOTAL</i>	210	630	10.5	5	0	2	3	0.5	0.0	0.2	0.3	0.2		
Collect samples	10													
Processing	180													
<i>Litter TOTAL</i>	190	570	9.5	30	19	21	29	3.2	2.0	2.2	3.1	2.6		
Lay tape measure	20													
Search quadrats	150													
Record data and release duplicates	20													
Processing	20													
<i>Quadrat TOTAL</i>	210	630	10.5	28	22	19	39	2.7	2.1	1.8	3.7	2.6		
Collect samples	90													
Processing	30													
<i>Tree beat TOTAL</i>	120	360	6	8	7	8	11	1.3	1.2	1.3	1.8	1.4		

Appendix 3f. *Mollusc species (Class Gastropoda) used in the test of the performance of the “best practice” approaches to monitoring collected from unburned (n = 4 forests) and burned (n = 4 forests) sites at Royal Natal National Park, KwaZulu-Natal, South Africa. M = micro-mollusc (Emberton et al., 1996), U = unburned and B = burned sites. Abundance scores are based on active search quadrat, litter sample and tree beat data.*

Sp.	Order	Family	Genus	species	Authority	M	U	B
1	Neritopsina	Hydrocenidae	<i>Hydrocena</i>	<i>noticola</i>	Benson, 1856	M	103	0
3	Eupulmonata	Pupillidae	<i>Lauria</i>	<i>dadion</i>	(Benson, 1864)	M	9	1
4	Eupulmonata	Orculidae	<i>Fauxulus</i>	<i>glanvilleanus (darglensis)</i>	(Ancey, 1888)	M	46	6
5	Eupulmonata	Orculidae	<i>Fauxulus</i>	<i>mcbeanianus</i>	Melville and Ponsonby, 1901	M	18	2
7	Eupulmonata	Vertiginidae	<i>Pupisoma</i>	<i>harpula</i>	(Reinhardt, 1886)	M	1	0
8	Eupulmonata	Vertiginidae	<i>Truncatellina</i>	<i>sykesii</i>	(Melville and Ponsonby, 1893)	M	11	0
9	Eupulmonata	Clausiliidae	<i>Macroptychia</i>	<i>africana</i>	(Melville and Ponsonby, 1899)		43	0
11	Eupulmonata	Streptaxidae	<i>Gulella</i>	<i>juxtidentis</i>	(Melville and Ponsonby, 1899)	M	67	3
12	Eupulmonata	Streptaxidae	<i>Gulella</i>	<i>mariae</i>	(Melville and Ponsonby, 1892)	M	1	0
13	Eupulmonata	Streptaxidae	<i>Gulella</i>	sp.		M	5	0
14	Eupulmonata	Rhytididae	<i>Nata</i>	<i>vernicaosa</i>	(Krauss, 1848)		8	1
16	Eupulmonata	Valloniidae	<i>Acanthinula</i>	sp.		M	19	4
17	Eupulmonata	Charopidae	<i>Afrodonta</i>	<i>novemlamellaris</i>	(Burnup, 1912)	M	13	1
18	Eupulmonata	Charopidae	<i>Trachycystis</i>	<i>contabulata</i>	Connolly, 1932	M	2	9
19	Eupulmonata	Charopidae	<i>Trachycystis</i>	<i>ectima</i>	(Melville and Ponsonby, 1899)	M	46	61
20	Eupulmonata	Charopidae	<i>Trachycystis</i>	<i>rudicostata</i>	Connolly, 1923	M	41	14
21	Eupulmonata	Charopidae	<i>Trachycystis</i>	<i>subpinguis</i>	Connolly, 1922		23	4
22	Eupulmonata	Charopidae	<i>Trachycystis</i>	<i>glanvilliana</i>	(Ancey, 1893)	M	0	4
24	Eupulmonata	Helicarionidae	<i>Kaliella</i>	<i>euconuloides</i>	Melville and Ponsonby, 1908	M	23	2
25	Eupulmonata	Euconulidae	<i>Afroconulus</i>	<i>diaphanus</i>	(Connolly, 1922)	M	0	5
26	Eupulmonata	Urocyclidae	<i>Sheldonia</i>	<i>transvaalensis</i>	(Craven, 1880)		9	21

4 A COMPARISON OF DIFFERENT APPROACHES TO PRIORITIZING FORESTS BASED ON INVERTEBRATE DIVERSITY

ABSTRACT

Systematic conservation planning aims to prioritize sites for meeting conservation objectives. Approaches to prioritizing areas for conservation investigated in this study include ranked species richness and complementarity. Forest dwelling, flightless invertebrates are of conservation importance because they have limited mobility and dispersal ability and should therefore be included in priority site analyses. This study aimed to investigate different approaches (selection criteria) and taxa for prioritizing Afrotropical forests in the Drakensberg Mountains, South Africa. The 17 forests sampled were ranked according to species richness and prioritized based on their complementarity using species data, taxonomic distinctness (orders, families and genera) and endemic mollusc and millipede species. There was no consistent trend in the priority ranking of forests based on species richness. Complementarity based on species richness only required eight forests spread among all reserves to represent all 62 flightless invertebrate species. The minimum set of forests identified by the complementarity analyses based on taxonomic distinctness and endemism, as opposed to species richness, did not capture all 62 flightless invertebrate species. I recommend augmenting the minimum set of sites identified using species complementarity with sites crucial for the survival of highly endemic species and species of conservation concern. Active management and protection of a range of forest patches across the north-south gradient of the Drakensberg is necessary to capture the region's exceptional diversity. Even small forest patches have conservation value and concern.

4.1 INTRODUCTION

It is seldom, if ever, possible to conserve all of each habitat type to maintain biodiversity and ecosystem processes (Lombard et al., 2003; Sarkar et al., 2004). Consequently, systematic conservation planning aims to prioritize sites to meet conservation objectives (Margules and Pressey, 2000). However, there is little agreement on the relative importance of different selection criteria for the prioritization of sites for conservation (Turpie, 1995). Examples of selection criteria include species diversity, species rarity, species priority, naturalness, area, economic value, and scientific value (Turpie, 1995).

Quantitative conservation targets predict how much has to be conserved to ensure the long-term persistence of biodiversity (Pressey et al., 2003). Targets allow the identification of priority areas for biodiversity conservation rather than focussing attention on the entire landscape (Driver et al., 2003a). In doing so, targets provide a clear purpose for

conservation decisions and make management decisions accountable and defensible (Pressey et al., 2003). Targets are normally set for biodiversity features and might include a given number of hectares of a vegetation type, or a number of occurrences of populations or species, or entire ecological systems (Margules et al., 2002; Driver et al., 2003a; Parrish et al., 2003).

One approach to prioritizing areas for conservation is to use simple, single-criterion scoring indices, where sites are ranked based on their species richness (Turpie, 1995; Church et al., 1996). Ranking based on species richness makes priority setting more systematic and explicit (Margules et al., 2002). Ranking works by ordering sites according to species richness and assigning the site with the highest richness the highest score.

A second approach to prioritization of areas uses iterative algorithms. Conservation planning studies based on iterative procedures have been used extensively in Australia and South Africa (Berliner and Benn, 2003). One such example is complementarity, which was introduced by Vane-Wright et al. (1991) and pioneered in Australia (Justus and Sarkar, 2002). Complementarity is a more widely employed approach for prioritization and conservation planning than scoring and ranking procedures. Complementarity describes differences among sites in terms of the species found in those sites and is therefore a measure of beta diversity (Magurran, 2004). Despite criticism for failure to address the complex issues of biodiversity persistence (Prendergast et al., 1999; Cowling et al., 2003), complementarity algorithms are no more reliant on high quality data than any other planning approach (Cowling et al., 2003) and they are only one of several stages in an explicit, defensible conservation plan (Margules and Pressey, 2000).

Complementarity scores are calculated using a variety of selection criteria, such as species, higher-taxa or endemic species data. Complementarity is based on algorithms that identify the minimum set of areas needed to maximise the diversity of a target taxon (Justus and Sarkar, 2002; Su et al., 2004). These algorithms add areas of highest complementarity in a stepwise fashion (Justus and Sarkar, 2002; Su et al., 2004) and have been referred to as critical faunas analysis (Ackery and Vane-Wright, 1984; Vane-Wright et al., 1991; Balmford et al., 1996b).

Complementarity using higher-taxon presence/absence as the selection criterion may be a cost effective way of rapidly surveying numerous, poorly known sites (Balmford et al., 1996b). Priority site networks selected using higher taxa require fewer sites than networks selected using species. Higher taxa (genera, families and orders) are also usually fewer in number and easier to distinguish between than their constituent species (Gaston, 2000).

Threatened and endemic species are other common selection criteria used in complementarity analyses. Most global prioritization schemes have focused on the patterns and occurrence of threatened and endemic species (Bonn et al., 2002). Threatened and endemic species contribute heavily to regional or local species assemblages. Endemic

species are often more reliant on conservation actions for their long-term survival than widespread species (Armstrong, 2002).

Complementarity is one approach within a suite of iterative heuristic methods that also include irreplaceability and flexibility (Church et al., 1996). Sites that are irreplaceable are those that support rare species or communities not found in any other site. Thus irreplaceable sites must be included in any reserve system that represents all species. Flexibility in selection of sites is desirable since selected sites might prove unsuitable due to factors not included in initial models. Iterative heuristic algorithms can be further refined for large areas and data sets by adding rules for selection, for example rules for including mandatory areas, forcing adjacency, and excluding undesirable areas (Lombard et al., 1997).

There are several alternative approaches to iterative heuristic methods. One approach is to select areas that maximise species coverage by reformulating a classic maximal covering location problem (MCLP) (Church et al., 1996). Another alternative is gap analysis, which can be used to prioritize sites for biodiversity conservation by assessing how well native vegetation types and animal species are represented in reserves (Kiestler et al., 1996). MCLP and gap analysis were not used in this study.

There are numerous different approaches to prioritization of areas for biodiversity conservation, but it is unknown which approach is most suitable for the prioritization of forest patches in the Drakensberg for invertebrate conservation. Each approach to prioritization has its own relative advantages and disadvantages. Different investigators and planners use different approaches. Therefore, a comparison among approaches and selection criteria is necessary to determine whether similar results are provided by the various approaches.

In existing nature reserves, such as the uKhahlamba-Drakensberg Park, prioritization is not aimed at identifying new sites to be conserved but rather the resource allocation decision would be the selection of a set of sites that collectively provides sufficient high-quality habitat to maintain viable populations of all native species (Church et al., 1996). Such resource allocation decisions are seldom made for invertebrates.

Invertebrates may comprise as much as 95% of biodiversity (Myers et al., 2000). Invertebrates should be included in priority site analyses because they are exceptionally diverse and drive many ecosystem processes (Armstrong, 2002). These processes include pollination, seed dispersal and nutrient cycling (Kremen et al., 1993). There are a high number of endemic invertebrate species in the Drakensberg Mountains, South Africa, many of which are palaeoendemics (Stuckenberg, 1962; Armstrong, 2002). These endemic species should be considered when identifying priority areas for conservation. In particular, forest dwelling, flightless invertebrates are of conservation importance because they have limited mobility and dispersal ability.

This study is only concerned with the value of sites for invertebrates and therefore considers only biological selection criteria (as opposed to economic or aesthetic criteria) for

prioritization of sites for conservation. Here, the relative merits of scoring techniques and iterative techniques are evaluated in terms of identifying the Afrotropical forests of prime conservation value for invertebrate conservation. A subset of forests within a protected area network was used for this preliminary investigation, with a view to the extension of these methods for prioritization of forests outside of protected areas in the Drakensberg. This study aimed to investigate different approaches and taxa to prioritizing Afrotropical forests based on flightless invertebrate diversity. This study had four objectives, namely to:

- 1) Prioritize forests using ranked species richness scores for all flightless invertebrate taxa combined and individual taxa;
- 2) Prioritize forests using complementarity based on
 - species presence/absence,
 - taxonomic distinctiveness (i.e. genera, families and orders) and
 - endemic species;
- 3) Investigate congruency among approaches in terms of priority forests, and
- 4) Identify characteristics of priority forests.

4.2 METHODS

4.2.1 Study sites

Seventeen Afrotropical forest patches were sampled during the summer of 2004/2005 in the KwaZulu-Natal Drakensberg. Study sites were located in four reserves within the uKhahlamba-Drakensberg Park: Rugged Glen Nature Reserve, Royal Natal National Park, Cathedral Peak and Injisuthi. Refer to Chapter 2.2.1 for details of study sites, which will hereafter be referred to as forests.

4.2.2 Sampling methods

Five sampling methods were used in each forest to collect flightless invertebrates. These sampling methods were soil samples, pitfall traps, leaf litter samples, active search quadrats and tree beats. Five invertebrate target taxa were sampled: molluscs, earthworms, centipedes, millipedes and ants. Refer to Chapter 2.2.2 for sampling methods.

4.2.3 Analyses

Prioritization of forests using ranked species richness

The 17 forests sampled were ranked according to their invertebrate species richness. The species richness of each forest was calculated as the number of species collected by the five sampling methods. Species richness was calculated for all target taxa combined and each taxon. The forest with the highest species richness was assigned a ranked value of 17, the

forest with the next highest species richness was assigned a ranked value of 16, and so on. Where two or more forests shared the same number of species, a shared ranked value was calculated as the mean of ranks for forests with the same number of species. If no species in a taxon was collected from a forest, a ranked value of zero was assigned to that forest for the taxon in question. The ranked scores for all forests for all taxa and each individual taxon were tabulated.

Prioritization of forests using species complementarity

The 17 forests sampled were prioritized based on their complementarity using species presence/absence data. Complementarity was calculated for all taxa combined and each taxon. An iterative algorithmic approach was used to establish the minimum number of forests needed to capture 100% of the species recorded (Ackery and Vane-Wright, 1984; Vane-Wright et al., 1991; Justus and Sarkar, 2002; Su et al., 2004). The first step was to select the forest with the highest number of species. The second step was to select the forest with the greatest taxonomic complement (i.e. the highest number of species not already accounted for in the first forest). In the event of ties, one forest was chosen. Step two was repeated until all species were accounted for at least once.

Prioritization of forests using taxonomic distinctness complementarity

The same algorithmic approach was used to prioritize the 17 forests based on taxonomic distinctness. Complementarity was calculated using three levels of taxonomic distinctness: orders, families and genera of all target taxa combined and each taxon. Ants were excluded because they were only identified to morphospecies and not genus or species level by the taxonomist.

Prioritization of forests using endemism complementarity

The 17 forests were also prioritized using the complementarity algorithm based on endemic mollusc and millipede species. Data were not available for other target taxa. Endemism analyses differed from species and taxonomic distinctness complementarity analyses because they were based on endemism scores and not presence/absence scores. Nineteen mollusc species were used for prioritization of forests using complementarity analyses based on endemism. Mollusc levels of endemism were scored using the mollusc endemism categories of Herbert and Kilburn (2004): central and southern Africa (score = 1), southern Africa (score = 2), South Africa (score = 3), eastern South Africa (score = 4), KwaZulu-Natal – Eastern Cape Province (score = 5), KwaZulu-Natal – Transkei (score = 6) and KwaZulu-Natal (score = 7) endemics. Eight millipede species were used for prioritization of forests using complementarity analyses based on endemism. Millipede levels of endemism were scored based on the four categories used by Hamer and Slotow (2002): South African (score

= 1), regional (score = 2), local (score = 3) and site (score = 4) endemics. Regional endemics refer to millipede species with distances of between 71 and 150 km separating the two furthest localities. Local endemics refer to millipede species with distances of 11 to 70 km separating the two furthest localities. Site endemics include all millipede species with only one locality and those with more than one locality but with 10 km or less separating the two furthest localities.

Congruency among approaches in terms of priority forests

The Kendall coefficient of concordance W was used to measure the relation or agreement among several rankings of the 17 forests (Siegel and Castellan, 1988). Kendall's W ranges between 0 (no agreement) and +1 (complete agreement). The significance of the observed W was determined by calculating chi-square with $N-1$ degrees of freedom. The Kendall coefficient of concordance and chi-square were calculated in SPSS for Windows, version 11.5 (SPSS, 2002).

Characteristics of priority forests

Characteristics of the top ten forests based on complementarity analyses were tabulated. Altitude and aspect were recorded in the field using a hand-held Garmin GPS and checked against 1:50 000 hiking maps for the uKhahlamba-Drakensberg Park. Slope was estimated as the distance from the lowest to the highest altitude point of each forest patch by counting the number of contour lines on the hiking maps. Mean annual precipitation (MAP) was obtained from Schulze (1997). Forest patch size (area) and distance to nearest sampled site were calculated using the GIS package ArcMap 8.3. Distances are straight-line distances between the center points of two forests. The relative influence of the characteristics of the top ten forests was examined with canonical correspondence analysis (CCA) using CANOCO 4.5 (Ter Braak and Šmilauer, 1998).

4.3 RESULTS

A total of 4797 individual specimens in 62 flightless invertebrate species were recorded in the 17 forests sampled. These 62 flightless invertebrate species comprised 25 mollusc, six earthworm, six centipede, 12 millipede and 13 ant species (Appendix 4a). In total, 35 genera, 27 families and 12 orders of target taxa were collected (Appendix 4b). Areas of endemism for mollusc and millipede species used in complementarity analyses are listed in Appendix 4a.

4.3.1 Prioritization of forests using ranked species richness

There was no consistent trend in the priority ranking of forests based on the species richness of all taxa combined and each taxon (Table 4.1). In general, the highest priority forests for each taxon were in the ten highest priority forests for all taxa combined.

Table 4.1. *Prioritization of forests using ranked species richness. Forests are ranked according to priority ranking for all target taxa combined. Rankings highlighted in grey are the highest priority forests for each taxon. RG = Rugged Glen Nature Reserve, RN = Royal Natal National Park, CP = Cathedral Peak and IN = Injisuthi. Numbers refer to the site number in each reserve.*

Rank	Forest	All taxa	Molluscs	Earthworms	Centipedes	Millipedes	Ants
1	IN 5	17	13	16.5	11.5	15	10.5
2	RN 3	16	15	14	15.5	11.5	6
3	IN 2	14.5	11.5	14	15.5	11.5	6
4	IN 3	14.5	15	0	6	17	10.5
5	IN 1	13	17	0	6	15	6
6	IN 4	12	10	9.5	6	11.5	13.5
7	RN 2	10.5	15	9.5	6	11.5	1
8	CP 3	10.5	11.5	16.5	11.5	5.5	2.5
9	RN 1	9	9	9.5	6	15	2.5
10	RG 1	8	4	9.5	15.5	5.5	17
11	RN 5	6.5	7	0	11.5	5.5	10.5
12	RN 6	6.5	5	9.5	11.5	5.5	13.5
13	RN 4	5	8	9.5	1	5.5	6
14	RN 7	4	6	0	15.5	1	10.5
15	RG 2	2.5	3	0	2	3	15.5
16	RG 3	2.5	1	0	6	5.5	15.5
17	RN 8	1	2	14	6	2	6

4.3.2 Prioritization of forests using complementarity

Only eight forests were needed to represent all 62 species at least once in the complementarity analysis based on the species presence/absence of all taxa combined (Table 4.2). The minimum set of forests identified by the complementarity analysis based on species presence/absence for all taxa combined included forests from all reserves sampled. All forests prioritized for earthworm, centipede and ant species were included in the minimum set of forests identified to represent all taxa combined. The forests with the highest mollusc (Injisuthi 1) and millipede (Injisuthi 3) species presence/absence were not included in the set of forests prioritized based on complementarity using species presence/absence for all taxa combined.

Table 4.2. *Prioritization of forests using complementarity based on species presence/absence, taxonomic distinctness and endemism scores. RG = Rugged Glen Nature Reserve, RN = Royal Natal National Park, CP = Cathedral Peak and IN = Injisuthi. The value in parentheses after the forest site for species and taxonomic distinctness is the number of taxa added by that forest. The value in parentheses after the forest site for endemism is the endemism score added by that forest.*

Taxon	Species	Taxonomic distinctness			Endemicity
		Genera	Families	Orders	
All taxa	IN 5 (36)	IN 5 (23)	IN 5 (22)	CP 3 (11)	
	RN 3 (11)	CP 3 (5)	CP 3 (4)	RN 3 (1)	
	RG 3 (5)	RN 3 (3)	RN 3 (1)		
	CP 3 (4)	IN 2 (1)			
	RG 1 (2)				
	RG 2 (1)				
	RN 6 (1)				
	IN 2 (1)				
Molluscs	IN 1 (18)	IN 5 (13)	IN 5 (12)	IN 5 (3)	RN 2 (60)
	RN 3 (5)	RN 3 (3)	RN 3 (2)		IN 1 (12)
	CP 3 (2)	CP 3 (1)			IN 3 (1)
Earthworms	IN 5 (3)	CP 3 (3)	CP 3 (3)	RN 3 (2)	
	RN 3 (1)	RN 3 (1)	RN 3 (1)		
	CP 3 (1)	IN 5 (1)			
	IN 2 (1)	IN 2 (1)			
Centipedes	RN 3 (6)	RN 3 (3)	RN 3 (2)	RN 3 (2)	
Millipedes	IN 3 (9)	IN 3 (6)	CP 3 (5)	CP 3 (4)	IN 3 (18)
	CP 3 (2)	CP 3 (2)	IN 3 (1)		CP 3 (6)
	IN 5 (1)	IN 5 (1)			
Ants	RG 1 (8)		RG 1 (1)	RG 1 (1)	
	RG 3 (2)				
	RG 2 (1)				
	RN 6 (1)				

The set of sites based on mollusc species presence/absence did not include the highest priority site for molluscs based on taxonomic distinctness or endemism. All species were included in the set of sites selected based on earthworm complementarity. All centipede species could be conserved by one forest only, and by using taxonomic distinctness based on centipede orders. The priority sites for millipedes based on taxonomic distinctness or endemism were included in the minimum set of sites for millipedes based on species presence/absence.

4.3.3 Congruency among approaches in terms of priority forests

Based on all complementarity analyses, ten forests were identified as priority forests. The top eight forests for molluscs, earthworms, centipedes and millipedes (Table 4.2) were all in the top ten forests prioritized according to ranked species richness for all taxa combined (Table 4.1). These top eight forests also included the highest ranked forest for each target taxon.

The Kendall coefficient of concordance W for the 20 analyses was significant ($W = 0.34$, $\chi^2_{1,16} = 108$, $P < 0.001$). A significant W implies that analyses are applying essentially the same standard in ranking the 17 forests. It was thus concluded with confidence that the agreement among the analyses was higher than it would have been by chance had their rankings been random or independent.

4.3.4 Characteristics of priority forests

No clear or consistent trend in any of the characteristics of the top ten priority forests based on complementarity was identified (Table 4.3). However, of the environmental correlates investigated, aspect, altitude and mean annual precipitation (MAP) appear to have the strongest influence on the species composition of priority sites (Figure 4.1). The first and second axes of the CCA accounted for 29.9% and 51.7% of the cumulative percentage variance of the species-environment relationship respectively. The variance inflation factors for all environmental variables were <10, showing no multicollinearity among environmental variables. The Monte Carlo test was non-significant for the first canonical axis ($F = 0.830$, $P = 0.140$) and all canonical axes ($F = 1.316$, $P = 0.084$), suggesting that an important environmental variable may be missing from the CCA.

Table 4.3. Characteristics of the top ten priority forests based on complementarity analyses. RG = Rugged Glen Nature Reserve, RN = Royal Natal National Park, CP = Cathedral Peak and IN = Injisuthi. Sites are ordered from north to south.

Site	Valley	MAP (mm)	Altitude (m a.s.l.)	Aspect	Area (ha)	Slope (m)	Distance to nearest sampled forest (km)
RG 1	Forest Walk	909	1400	S	3.46	60	0.137
RG 2	Forest Walk	878	1400	S	2.70	40	0.137
RG 3	Forest Walk	878	1400	S	1.14	20	0.268
RN 2	Thukela Gorge	1327	1600	S	14.00	70	0.344
RN 3	Thukela Gorge	1327	1620	S	7.64	110	0.302
RN 6	Devil's Hoek	1225	1620	SSE	12.00	40	0.456
CP 3	Rainbow Gorge	1167	1550	S	21.80	100	26.257
IN 1	Yellowwood Forest	1022	1500	SSW	1.41	40	1.114
IN 3	van Heyningen's Pass	1022	1600	S	5.28	80	0.400
IN 5	van Heyningen's Pass	1076	1650	S	2.41	80	0.362

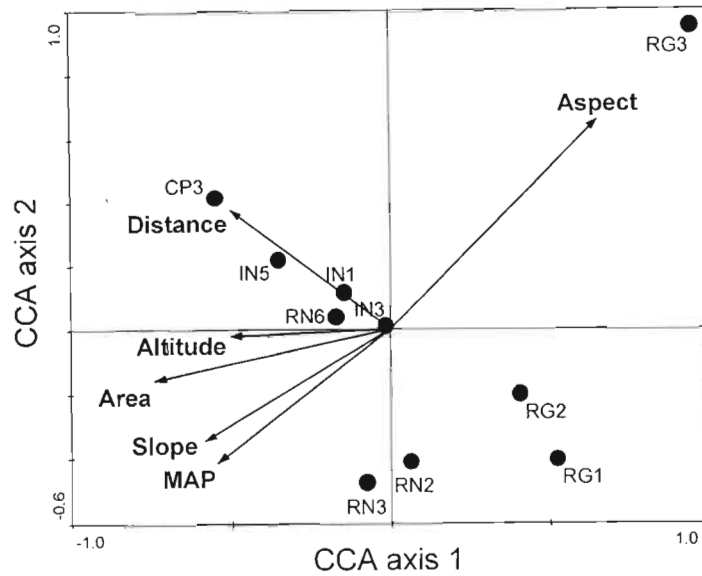


Figure 4.1. Canonical correspondence analysis (CCA) of priority sites and environmental variables. Axes 1 and 2 account for 51.7% of the cumulative percentage variance of the species-environment relationship. Vectors indicate the direction of influence of the environmental variables. RG = Rugged Glen, RN = Royal Natal, CP = Cathedral Peak and IN = Injisuthi. Sites and environmental variables correspond with Table 4.3.

4.4 DISCUSSION

From a management perspective, the approach and selection criterion that prioritize the maximum diversity in the minimum number of sites is desirable because resources available for conservation are limited. In this study, the ranked species richness approach included all 17 forests whereas complementarity based on species presence/absence only required eight forests to represent all 62 invertebrate species.

Complementarity is therefore a more desirable approach than ranked scores for prioritizing Afrotemperate forests for flightless invertebrate conservation in the Drakensberg. Scoring and ranking procedures have also been criticised for their inability to significantly improve efficiency over ad hoc representation (Margules et al., 2002). Turpie (1995) also found that the iterative (complementarity) approach is more efficient than the single-criterion scoring and ranking approach in selecting a network of reserves that conserves all target species of estuarine waterbirds in South Africa.

Although the use of minimum sets of priority areas is appealing, representing each species only once is not a sensible planning strategy (Gaston et al., 2001). Measures of species richness often fail to provide information regarding the representativeness of a set of conservation areas (Su et al., 2004). Complementarity based on species presence/absence alone treats all species as equal, rather than weighting endemic and threatened species that need more urgent conservation action (Su et al., 2004). A more sensible planning strategy is

to augment the minimum set of sites identified using complementarity based on species presence/absence. This could be achieved by adding sites that are crucial for the survival of highly endemic species and threatened species. Depending on the status of a species, all sites in which that species occurs may need to be actively conserved.

Consideration of endemism cannot be divorced from conservation because endemic species have a higher probability of facing extinction. Endemic species tend to have smaller range sizes and lower abundances than non-endemic species (Gaston, 1994). Priority areas based on the occurrence of endemic species make the presumption that these areas will also provide adequate protection for the majority of other species (Bonn et al., 2002). However, South African bird distribution data have shown that focussing priority area selection on endemic species does not guarantee the representation of all other species (Bonn et al., 2002). Therefore, endemic species should be used with caution when selecting priority sites for wholesale biodiversity conservation.

In forests of the Drakensberg Mountains, taxonomic distinctness appears to be a suitable surrogate for species presence/absence of millipedes but not molluscs. However, the minimum set of sites identified for either molluscs or millipedes was not a suitable surrogate for species presence/absence of all flightless invertebrate taxa investigated in this study. Where resources permit, taxonomic experts are available and/or identification to the level of species is feasible, it is best to base site prioritization on species presence/absence. Nevertheless, higher taxon surrogates can substantially reduce the costs of surveys by reducing the costly nature of species identifications (Pik et al., 1999; Ward and Larivière, 2004).

The use of higher taxa as surrogates for species richness has received varying recommendations in the literature. Balmford et al. (1996b) found that species-based algorithms contained only 2% more woody plant species in Sri Lankan forests than genus-based priority selection. Balmford et al. (1996b) promote the use of genus-based algorithms for priority site selection because genus-level identification saved roughly 60% of the cost of identifying woody plants to species level. Andersen (1995) does not recommend the use of genus-based algorithms for priority site selection. Andersen (1995) found that the relationship between ant species richness and ant genus richness had poor predictive power. Genus richness was therefore an unreliable surrogate for species richness in Australian ant faunas. Ultimately, the success of higher taxa as surrogates for species will depend on the nature of the taxa under investigation. Unfortunately, Andersen's (1995) results suggest that higher-taxon surrogacy would be least reliable for the very organisms that it would most benefit – the invertebrates. My study concurs with Andersen's (1995) conclusion.

Identifying characteristics of priority forest sites for flightless invertebrate conservation is not an easy task. Nevertheless, Howard et al. (1998) found that in Uganda, different taxa exhibit similar biogeography, so priority forests for one taxon collectively also represent the

important forest types for other taxa. Although not specifically tested in this study, ground dwelling forest invertebrates in the Drakensberg are expected to show similar biogeographic patterns of distribution. Invertebrate distributions are also likely to be determined by species-specific fine-scale combinations of biotic and abiotic factors. Of the six environmental variables included in this study, aspect, patch area and mean annual precipitation (MAP) appear to be important determining factors of invertebrate species richness. This implies that even small forest patches are of conservation value and concern. Furthermore, active management and protection of a range of forest patches across the north-south gradient of the Drakensberg is needed to capture the region's exceptional diversity. Missing environmental variables might include soil type, soil depth, soil moisture, soil calcium availability (particularly for molluscs), tree and shrub species composition, and other fine-scale habitat variables.

A final caveat should be added since only 17 forests were sampled in this study; a small subset of the total number of forest patches in the region. A more inclusive study would involve modelling species distribution, diversity and environmental correlates using data from forests throughout the Drakensberg region. This study will hopefully provide guidance and stimulus for future conservation planning exercises for flightless invertebrate conservation in the Drakensberg. This study was intended only as a preliminary investigation and should be viewed in this context.

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Appendix 4a. List of all mollusc, earthworm, centipede, millipede and ant species used in prioritization analyses. Mollusc endemism is based on the eight categories used by Herbert and Kilburn (2004). Millipede endemism is based on the four categories used by Hamer and Slotow (2002).

Sp.	Order	Family	Genus	species	Authority	Area of endemism
Class Gastropoda						
1	Neritopsina	Hydrocenidae	<i>Hydrocena</i>	<i>noticola</i>	Benson, 1856	South Africa
2	Architaenioglossa	Cyclophoridae	<i>Chondrocyclus</i>	<i>isipingoensis</i>	(Sturany, 1898)	South Africa
3	Eupulmonata	Pupillidae	<i>Lauria</i>	<i>dadion</i>	(Benson, 1864)	South Africa
4	Eupulmonata	Orculidae	<i>Fauxulus</i>	<i>glanvilleanus (darglensis)</i>	(Ancey, 1888)	KZN-Eastern Cape
5	Eupulmonata	Orculidae	<i>Fauxulus</i>	<i>mcbeanianus</i>	Melville and Ponsonby, 1901	KZN
7	Eupulmonata	Vertiginidae	<i>Pupisoma</i>	<i>harpula</i>	(Reinhardt, 1886)	Afro-Asian
8	Eupulmonata	Vertiginidae	<i>Truncatellina</i>	<i>sykesii</i>	(Melville and Ponsonby, 1893)	southern Africa
9	Eupulmonata	Clausiliidae	<i>Macroplychia</i>	<i>africana</i>	(Melville and Ponsonby, 1899)	South Africa
10	Eupulmonata	Achatinidae	<i>Archachatina</i>	sp.		
11	Eupulmonata	Streptaxidae	<i>Gulella</i>	<i>juxtidentis</i>	(Melville and Ponsonby, 1899)	KZN
12	Eupulmonata	Streptaxidae	<i>Gulella</i>	<i>mariae</i>	(Melville and Ponsonby, 1892)	KZN-Eastern Cape
13	Eupulmonata	Streptaxidae	<i>Gulella</i>	sp.		
14	Eupulmonata	Rhytidae	<i>Nata</i>	<i>vernica</i>	(Krauss, 1848)	southern Africa
15	Eupulmonata	Rhytidae	<i>Natalina</i>	sp.		
16	Eupulmonata	Valloniidae	<i>Acanthinula</i>	sp.		
17	Eupulmonata	Charopidae	<i>Afrodonta</i>	<i>novemlamellaris</i>	(Burnup, 1912)	central and southern Africa
18	Eupulmonata	Charopidae	<i>Trachysystis</i>	<i>contabulata</i>	Connolly, 1932	KZN-Transkei
19	Eupulmonata	Charopidae	<i>Trachysystis</i>	<i>ectima</i>	(Melville and Ponsonby, 1899)	KZN
20	Eupulmonata	Charopidae	<i>Trachysystis</i>	<i>rudicostata</i>	Connolly, 1923	central and southern Africa
21	Eupulmonata	Charopidae	<i>Trachysystis</i>	<i>subpinguis</i>	Connolly, 1922	South Africa
22	Eupulmonata	Charopidae	<i>Trachysystis</i>	<i>glanvilliana</i>	(Ancey, 1893)	eastern South Africa
24	Eupulmonata	Helicarionidae	<i>Kaliella</i>	<i>euconuloides</i>	Melville and Ponsonby, 1908	KZN
25	Eupulmonata	Euconulidae	<i>Afroconulus</i>	<i>diaphanus</i>	(Connolly, 1922)	central and southern Africa
26	Eupulmonata	Urocyclidae	<i>Sheldonia</i>	<i>transvaalensis</i>	(Craven, 1880)	South Africa
27	Eupulmonata	Achatinidae	<i>Archacatina</i>	<i>dimidiata</i>	(Smith, 1878)	South Africa
Class Oligochaeta						
254	Haplotaxida	Acanthodrilidae	<i>Dichogaster</i>	sp.		
255	Haplotaxida	Acanthodrilidae	<i>Parachilota</i>	sp. 1		
259	Haplotaxida	Lumbricidae	<i>Apporectodea</i>	<i>rosea</i>	(Savigny, 1826)	
260	Haplotaxida	Lumbricidae	<i>Dendrodrius</i>	<i>rubidus</i>	(Savigny, 1826)	
261	Haplotaxida	Megascolecidae	<i>Amyntas</i>	sp.		
262	Opisthopora	Microchaetidae	<i>Proandricus</i>	sp.		
Class Chilopoda						
45	Geophilomorpha	Geophilidae	<i>Rhysida</i>	<i>afra (afra)</i>	(Peters, 1855)	
47	Geophilomorpha	Geophilidae	<i>Rhysida</i>	sp. 2		
48	Geophilomorpha	Geophilidae	<i>Rhysida</i>	sp. 1		
49	Lithobiomorpha	Henicopidae	<i>Paralamyctes</i>	<i>spenceri</i>	Pocock, 1902	
50	Lithobiomorpha	Henicopidae	<i>Lamyctes</i>	<i>africana</i>	(Porat, 1971)	
51	Lithobiomorpha	Henicopidae	<i>Lamyctes</i>	sp.		
Class Diplopoda						
32	Sphaerotheirida	Sphaerotheiridae	<i>Sphaerotherium</i>	<i>perbrincki</i>	Schubart, 1958	Site
33	Sphaerotheirida	Sphaerotheiridae	<i>Sphaerotherium</i>	<i>dorsale</i>	(Gervais, 1847)	South Africa
34	Sphaerotheirida	Sphaerotheiridae	<i>Sphaerotherium</i>	<i>mahaum</i>	Schubart, 1958	Site
35	Sphaerotheirida	Sphaerotheiridae	<i>Sphaerotherium</i>	sp.		
36	Polydesmida	Dalodesmidae	<i>Gnomeskelus</i>	sp.		
37	Polydesmida	Gomphodesmidae	<i>Ulodesmus</i>	<i>simplex</i>	Lawrence, 1953	Site
38	Polydesmida	Gomphodesmidae	<i>Gnomeskelus</i>	<i>montivagus</i>	Verhoeff, 1939	Local
39	Polydesmida	Gomphodesmidae	<i>Gnomeskelus</i>	<i>attemsii</i>	Verhoeff, 1939	Regional
40	Spirostreptida	Odontopygidae	<i>Spinotarsus</i>	sp. 2		
41	Spirostreptida	Odontopygidae	<i>Spinotarsus</i>	sp. 1		
43	Spirostreptida	Spirostreptidae	<i>Doratogonus</i>	<i>montanus</i>	Hamer, 2000	Regional
44	Polyzoniida	Siphonotidae	<i>Rynchomecogaster</i>	<i>lawrencei</i>	Verhoeff, 1939	Site
Class Insecta						
53	Hymenoptera	Formicidae		sp. 1		
54	Hymenoptera	Formicidae		sp. 2		
56	Hymenoptera	Formicidae		sp. 4		
57	Hymenoptera	Formicidae		sp. 5		
58	Hymenoptera	Formicidae		sp. 6		
59	Hymenoptera	Formicidae		sp. 7		
60	Hymenoptera	Formicidae		sp. 8		
61	Hymenoptera	Formicidae		sp. 9		
62	Hymenoptera	Formicidae		sp. 10		
63	Hymenoptera	Formicidae		sp. 11		
64	Hymenoptera	Formicidae		sp. 12		
65	Hymenoptera	Formicidae		sp. 13		

Appendix 4b. Orders, families and genera of molluscs (Class Gastropoda), earthworms (Class Oligochaeta), centipedes (Class Chilopoda), millipedes (Class Diplopoda) and ants (Class Insecta) used in complementarity analyses based on taxonomic distinctness.

Taxon	Order	Family	Genus
Mollusc	Neritopsina	Hydrocenidae	<i>Hydrocena</i>
Mollusc	Architaenioglossa	Cyclophoridae	<i>Chondrocyclus</i>
Mollusc	Eupulmonata	Pupillidae	<i>Lauria</i>
Mollusc	Eupulmonata	Orculidae	<i>Fauxulus</i>
Mollusc	Eupulmonata	Vertiginidae	<i>Pupisoma</i>
Mollusc	Eupulmonata	Vertiginidae	<i>Truncatellina</i>
Mollusc	Eupulmonata	Clausiliidae	<i>Macroptychia</i>
Mollusc	Eupulmonata	Achatinidae	<i>Archacatina</i>
Mollusc	Eupulmonata	Streptaxidae	<i>Gulella</i>
Mollusc	Eupulmonata	Rhytidae	<i>Nata</i>
Mollusc	Eupulmonata	Rhytidae	<i>Natalina</i>
Mollusc	Eupulmonata	Valloniidae	<i>Acanthinula</i>
Mollusc	Eupulmonata	Charopidae	<i>Afrodonta</i>
Mollusc	Eupulmonata	Charopidae	<i>Trachycystis</i>
Mollusc	Eupulmonata	Helicarionidae	<i>Kaliella</i>
Mollusc	Eupulmonata	Euconulidae	<i>Afroconulus</i>
Mollusc	Eupulmonata	Urocyclidae	<i>Sheldonia</i>
Mollusc	Eupulmonata	Vertiginidae	<i>Pupisoma</i>
Mollusc	Eupulmonata	Pupillidae	<i>Pupilla</i>
Earthworm	Haplotaxida	Acanthodrilidae	<i>Dichogaster</i>
Earthworm	Haplotaxida	Acanthodrilidae	<i>Parachilota</i>
Earthworm	Haplotaxida	Lumbricidae	<i>Octolasion</i>
Earthworm	Haplotaxida	Lumbricidae	<i>Apporectodea</i>
Earthworm	Haplotaxida	Lumbricidae	<i>Dendrodrilus</i>
Earthworm	Haplotaxida	Megascolecidae	<i>Amyntas</i>
Earthworm	Opisthopora	Microchaetidae	<i>Proandricus</i>
Centipede	Geophilomorpha	Geophilidae	<i>Rhysida</i>
Centipede	Lithobiomorpha	Henicopidae	<i>Paralamyctes</i>
Centipede	Lithobiomorpha	Henicopidae	<i>Lamyctes</i>
Millipede	Sphaerotheriida	Sphaerotheriidae	<i>Sphaerotherium</i>
Millipede	Polydesmida	Dalodesmidae	<i>Gnomeskelus</i>
Millipede	Polydesmida	Gomphodesmidae	<i>Ulodesmus</i>
Millipede	Polydesmida	Gomphodesmidae	<i>Gnomeskelus</i>
Millipede	Spirostreptida	Odontopygidae	<i>Spinotarsus</i>
Millipede	Spirostreptida	Spirostreptidae	<i>Doratogonus</i>
Millipede	Polyzoniida	Siphonotidae	<i>Rynchomecogaster</i>
Ant	Hymenoptera	Formicidae	

5 CONSERVATION PLANNING AND MANAGEMENT RECOMMENDATIONS FOR FLIGHTLESS INVERTEBRATES IN AFROTEMPERATE FOREST

Forests in the Drakensberg Mountains, although generally small and fragmented, represent a wealth of globally significant biodiversity. These forests have high conservation value because they provide essential ecosystem services, including water retention and purification, flood attenuation and carbon sequestration (Berliner, 2005). Forest dwelling invertebrates are also critically important in ecosystem functioning because of the wealth of services they provide, including nutrient recycling, decomposition, plant pollination, pest control, and food for other animals. Many forest invertebrates have more localised distributions than other taxa. Therefore, forest dwelling invertebrates also have conservation value and should be included in conservation planning and management exercises.

5.1 Summary of findings

Spatial and seasonal scales in combination are the key to the evaluation of natural change (Heywood and Iriondo, 2003). These scales are important in terms of evolutionary change and ecological dynamics and in terms of human impacts on nature. This study produced spatially explicit fine-scale (i.e. patch level comparison) data, which will provide guidance for future conservation planning. I conclude that Drakensberg Afrotemperate forests should be managed at the spatial scale of sites, i.e. areas <10 km (sensu Hamer and Slotow, 2002) or within valleys because at greater scales (across valleys), species turnover increases.

The results from this study have shown that flightless invertebrate species richness and community structure in forests of the Drakensberg are influenced by natural seasonal fluctuations in the environment. Therefore, the season in which sampling takes place should be considered for both biodiversity assessment and monitoring for the impact of management actions, and conservation planning in general. The data from this study show that sampling should take place during the wet season, when the highest number of species was recorded, and repeated sampling through the year is unnecessary for the focus taxa since the species sampled during the dry season were simply a subset of those collected in the wet months. Molluscs are potentially the most suitable surrogate taxon for flightless invertebrate diversity and for monitoring the impact of disturbance in the form of fire, and leaf litter samples and active search quadrats are the most suitable sampling methods for biodiversity assessments and monitoring programmes for flightless invertebrate conservation in Afrotemperate forest in the Drakensberg Mountains. "Best practice" approaches identified in this study also provide an interface between science and conservation management decision-making and are intended to promote informed management decisions for

biodiversity conservation. The “best practice” approaches to biodiversity assessment and monitoring for flightless invertebrate conservation are, therefore, the most valuable outcome of this study.

Using different criteria for prioritizing forests based on ground dwelling invertebrates results in different sets of forests being selected. The minimum set of sites identified using complementarity based on species presence/absence augmented with taxa of conservation importance (i.e. highly endemic species) appears to be the most rigorous investigated approach to prioritizing Afrotemperate forest patches in the KwaZulu-Natal Drakensberg for flightless invertebrate conservation.

5.2 Recommendations based on results of this study

5.2.1 *Recommendations for future sampling*

The study presented here should be viewed as a preliminary effort to address relevant questions for which no appropriate data existed previously. Data limitations are a major impediment to developing a perfect conservation plan (Noss, 2004). Basic species and locality data should be included in conservation planning (Brooks et al., 2004), but are currently inadequate for the Drakensberg. Although material has been collected from the forests in the past, much of the data for museum specimens does not include sufficiently detailed locality data, and in addition, most material has simply been collected opportunistically and there is no indication of sampling effort. These issues make existing data difficult to use in conservation planning with any confidence.

A goal for future invertebrate conservation is (1) the wise use of a set of standardized sampling methods with enough replicates so that conventional statistics can be used, (2) to collect and study a relatively limited number of taxa, (3) in a variety of habitats and ecosystems within the region under study (Ward and Larivière, 2004). For the flightless invertebrate fauna studied, additional forests need to be sampled and within each forest, additional sites require increased sampling effort. The protocols identified in the “best practice” approaches to biodiversity assessment and monitoring based on seasonal sampling in this study provides guidance in terms of the timing and methods that will provide appropriate data. The actual number of forests and replicates in each forest required to adequately sample the fauna requires separate investigation.

Additional sampling to fill in the spatial gaps between areas sampled in this study is recommended to improve our spatial understanding of the distribution patterns of flightless invertebrates in the Drakensberg. It is especially important to survey the invertebrate biodiversity of the Upper Thukela region (which is currently not formally protected by the uKhahlamba-Drakensberg Park but does support Afrotemperate forest patches; Ezemvelo

KZN Wildlife, 2005) for viable populations of invertebrates of conservation priority, such as Red Listed and local endemic species.

Further investigation of possible effects of environmental factors on invertebrate species turnover among forest patches is also recommended, since these factors may have as great an impact on turnover as distance between forests. Future studies should collect habitat data (such as edge width, core area, tree and shrub species composition, soil depth and type) from each forest patch, which will allow the identification of key factors for flightless ground dwelling invertebrate diversity, which in turn will allow predictive species and community distribution modelling. This would address the problem associated with surveying all forests in the region thoroughly for conservation.

5.2.2 Application of species and locality data collected in quantified sampling

The data collected on species presence/absence, community structure, species richness, and the environmental factors associated with ground dwelling invertebrate diversity in forest have application in several steps in systematic conservation planning. These are the setting of conservation targets (Margules and Pressey, 2000; Driver et al., 2003a; Driver et al., 2005), the prioritization of biodiversity features (localities or sites of a particular vegetation type and species in this case) (Driver et al., 2003a) in order to achieve the target, and monitoring the maintenance these features. Efforts to include ground dwelling flightless invertebrates in conservation planning activities for the Drakensberg are presented below, as well as recommendations for improving these, based on the findings of the research presented in the thesis.

5.2.3 Recommendations for the successful inclusion of invertebrates in conservation planning

The importance of invertebrates in terms of ecosystem functioning and endemism is increasingly becoming recognised amongst conservation planners and practitioners. The main current constraint on invertebrate conservation is the need for appropriate information provided in a format that allows its integration into various activities.

5.3 Targets for invertebrate conservation in Afrotropical forest

5.3.1 The KwaZulu-Natal Systematic Conservation Plan

The KwaZulu-Natal Systematic Conservation Plan makes the assumption that protected areas will continue to conserve key species and habitats at the same level at which they occurred when the plan was developed (Ezemvelo KZN Wildlife, 2005). If this assumption fails, then provincial conservation targets will not be achieved. Montane *Podocarpus* Forest is one of the vegetation types for which the uKhahlamba-Drakensberg Park is essential in

order to meet provincial conservation targets (Ezemvelo KZN Wildlife, 2005). The Montane black millipede, *Doratogonus montanus*, collected in this study is also one of the species included in the provincial conservation targets (Ezemvelo KZN Wildlife, 2005). However, no formal monitoring programmes for either this vegetation type or millipede are currently in place.

5.3.2 *Quantitative and qualitative targets for invertebrate conservation*

Targets strengthen the efficiency of successive stages in conservation planning (Pressey et al., 1993) by making conservation decisions accountable and defensible (Pressey et al., 2003). To set quantitative and qualitative targets for invertebrate diversity conservation in Afrotropical forest four questions need to be addressed. Firstly, which species have sufficient information to accurately map their distribution over the Drakensberg? Secondly, how many patches are required to conserve invertebrate biodiversity pattern and ecological process? Thirdly, which invertebrate species are of special concern? Lastly, how many populations of a species are needed to ensure survival of the species?

Insufficient empirical data are available to adequately answer any of these questions with any degree of confidence. A safe assumption would be to conserve as many patches and populations as possible (Primack, 2000) to conserve the full complement of invertebrate species. There is no internationally agreed conservation target value that can be applied to forests (Berliner and Benn, 2003), but baseline targets such as the IUCN 10% rule, 15% of each landscape type in New South Wales (Pressey et al., 1997) and 15% of the forest types in KwaZulu-Natal under strict protection (Goodman, 2002) have been implemented. Baseline targets have been criticised for being too simplistic and implying that all elements of biodiversity have equal conservation importance (Berliner and Benn, 2003). An alternative solution is to set graduated targets by adjusting a base target value with weightings calculated using the level of threat and extent of transformation of each vegetation type. This approach has been successfully implemented in conservation planning projects such as CAPE, the Cape Action Plan for the Environment (Pressey et al., 2003) and for the forest biome in South Africa (Berliner, 2005). Using a minimum baseline target value of 15%, an overall target value of 63.5% was set for Drakensberg Montane Forest (Berliner, 2005). However, only 47.3% of Drakensberg Montane Forest is currently under some form of protection, so the target shortfall is 25.5% (312 ha).

The recommended value of 63.5% of forests may be adequate to conserve the flightless invertebrate fauna of the Drakensberg forests, but the other recommended baseline values of 10% and 15% may not. This would be related to species turnover between forests, and only taxa with low levels of turnover would be adequately conserved by the lower percentages. While the aim of this part of the thesis was not to actually set targets, complementarity analysis may provide some insight as a starting point for further study. This

analysis indicated that eight of the 17 forests were required to conserve all sampled species, which is 47% of the sampled forests, but further investigation into how many forests are required to represent each species more than once is still required. In addition, sampling of more forests and the inclusion of more species data are required to determine the validity of using only a limited data set for setting a target. Of course which forests are selected to make up the target percentage also requires discussion because different approaches give different answers.

Ezemvelo KZN Wildlife manages a database of spatial localities of all known species, with thousands of records throughout the province. However, for accurate mapping of flightless invertebrates there is insufficient information for most species and most existing data are outdated (Armstrong pers. comm., 2006).

Identifying species of special concern (i.e. endemic, near endemic, endangered and rare species) is difficult because most invertebrate species are data deficient. Twenty-four millipede and four mollusc species are endemic to the Drakensberg forests (Ezemvelo KZN Wildlife, 2005). At least one Red Listed, critically endangered species, *C. burnupi*, is also restricted to Afrotropical forest (Herbert and Kilburn, 2004). Drakensberg forests are therefore of significant conservation importance for invertebrates, although not so for vertebrates (Eeley et al., 2001). At present, the only invertebrates included in the provincial Ezemvelo KZN Wildlife C-Plan are 28 species of millipedes (Oellermann pers. comm., 2006). However, the organisation is currently in the process of incorporating many more invertebrates. Therefore, now is a key time in which to undertake more intensive invertebrate surveys to provide accurate data for mapping.

For each target species, as a bare minimum estimate, three viable populations of species of conservation value and concern should be conserved (Armstrong, 2002; Berliner and Benn, 2003). For detritivorous and herbivorous invertebrates, 10 000 individuals might be considered a viable population (Primack, 2000; Armstrong pers. comm., 2006). For predatory invertebrates such as onychophorans and chlamydephorid slugs, the estimate for a viable population would be lower. However, in the absence of detailed demographic studies, accurate estimates of minimum viable populations cannot be made (Primack, 2000).

5.3.3 *Management recommendations for achieving these targets*

Preliminary indications are that fire has a negative impact on flightless, ground dwelling invertebrate diversity. Forests should not be burned unless forest fires occur naturally and forest ecotones must be maintained. Outside of natural fire refugia (such as deep, steep sided gorges) forest margins act as natural buffers, insulating forests from burns (von Maltitz et al., 2003).

Forest patches cannot survive in isolation, so it is important to manage the grassland, riverine vegetation, forest ecotone and forests holistically. Loss of grassland can result in

loss of important forest invertebrates that move between grassland and forest such as *D. montanus* and other invertebrate taxa such as honey bees that nest in forest and are keystone grassland species (Armstrong pers. comm., 2006). Kotze and Samways (1999) and Bourquin (2001) both established that disturbance in the surrounding habitat matrix effects the composition and dynamics of forest invertebrate communities.

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