DISTRIBUTION PATTERNS OF EPIGAEIC INVERTEBRATES IN AN AFROMONTANE FOREST-GRASSLAND MOSAIC IN KWAZULU-NATAL, SOUTH AFRICA

by

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Distribution patterns of epigaeic invertebrates in an Afromontane forest-grassland mosaic in KwaZulu-Natal, South Africa

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This thesis is based on the following articles which will be referred to in the text by their Roman numerals:

I Kotze, D.J. and Samways, M.J. 1999. Support for the multi-taxa approach in biodiversity assessment, as shown by epigaeic invertebrates in an Afromontane forest archipelago. *Journal of Insect Conservation* **3**, 125-143.

II Kotze, D.J. and Samways, M.J. 1999. Invertebrate diversity at forest-grassland ecotones in an Afromontane forest landscape in South Africa. - Submitted

III Kotze, D.J. and Samways, M.J. 1999. Inter-seasonal consistency in spatial pattern of invertebrates across a forest patch-grassland matrix ecotone in KwaZulu-Natal, South Africa. - Submitted

IV Kotze, D.J. and Samways, M.J. 1999. Invertebrate conservation at the interface between the grassland matrix and natural Afromontane forest fragments. *Biodiversity and Conservation* **8**, 1339-1363.

In my PhD thesis I have studied the abundance and species richness of various epigaeic invertebrates (in particular terrestrial amphipods, carabids and ants) in Afromontane forests and grasslands and at the interface between these two systems. The field work for the thesis was done in 1993-1996.

PREFACE

This study and preparations for this thesis were done while the author was a full-time student in the School of Botany and Zoology, University of Natal, South Africa, from July 1993 to November 1997, with Professor M.J. Samways as supervisor.

This thesis, unless specifically referred to in the text, is my own original work, and has not been submitted in any other form to another University.

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General abstract

Considered key landscape elements, ecotones play an important role in landscape ecology. In heavily fragmented, or heterogeneous landscapes, ecotones become a major, even dominant, feature. Yet, there are relatively few studies investigating communities of invertebrates associated with ecotones, especially across natural boundaries. Furthermore, most analyses of habitat loss do not consider the characteristics of the areas surrounding remaining habitat, the matrix. This thesis attempts to partially fill the gap.

Afromontane forest-grassland ecotones are characteristically sharp (usually a few metres), are mainly fire-maintained, and have been in existence for, perhaps, millions of years. Therefore they provide a good opportunity to study ecotone, forest patch and grassland matrix characteristics together, and the associated species assemblages. In short, I investigated the diversity and distribution patterns of epigaeic invertebrates across ecotones between the natural and isolated patches of Afromontane forests and the surrounding natural grassland matrix, in the province of KwaZulu-Natal, South Africa.

In particular, the following primary hypothesis was evaluated; do edge effects, in terms of elevated abundance and species richness, and in terms of abrupt, significant changes in environmental conditions, occur across near-natural ecotones. These edge effects quite often occur across anthropogenically-created habitat junctions, but it is not clear whether they do across natural ones.

To test this hypothesis, the following secondary hypotheses were evaluated. Firstly, often a single invertebrate taxon is used for assessing changing landscape patterns. However, recent work has suggested that patterns and responses vary widely between taxa, and that management programmes based on the knowledge of a single taxon would not necessarily predict or safeguard that of others. Therefore, in chapter I, the hypothesis whether a single taxon could be used in biodiversity studies, or alternatively, whether it is better to select an array of taxa, was tested. Several invertebrate taxa were selected to investigate this. These included terrestrial amphipods, spiders, carabids, staphylinids and ants. Indeed, results showed that species diversities and assemblage-compositions of epigaeic spiders, carabids, staphylinids and ants were significantly different in different-sized Afromontane forest patches. Only carabids and staphylinids correlated positively with each other in terms of numbers of species. The other taxa showed only weak positive, or negative, correlations in their species richness. Results supported the multi-taxa approach in conservation studies, even among groups sharing a common habitat stratum.

Secondly, organismal diversity usually increases at disturbed habitat edges. This phenomenon is commonly referred to as the biological edge effect. This pattern, however, is not universal and a number of authors have shown evidence contradicting this hypothesis. In chapter II amphipods, ground beetles and ants were collected to test the biological edge effect hypothesis. In addition, a number of abiotic factors were measured across these forest-grassland boundaries in an attempt to relate the biotic with the abiotic. Little evidence was found to support the classical edge-effect hypothesis (elevated species richness at the ecotone). In fact, carabid abundance and species richness was high in forests, decreasing gradually through the ecotone to a low in grasslands. In contrast, ant species richness increased significantly from a low in forests, increasing gradually through the ecotone, to a high in grasslands. Certain species did, however, show a significant increase in abundance at the ecotone, such as *Talistroides africana*, a terrestrial amphipod, and *Tetramorium avium*, a seed-predatory ant. Afromontane forest-grassland ecotones are natural and are not the result of anthropogenic clear-cut fragmentation. They also lacked any great changes in micro-environmental conditions. I hypothesise that edge effects are of less importance at more naturally-maintained habitat boundaries even if these boundaries are sharp.

Thirdly, climatic variation has a major impact on invertebrate communities. The Afromontane landscape experiences hot and wet summers, and cool and dry winters. I hypothesised that invertebrate distribution patterns across an ecotone change from one season to the next (chapter III). For example, it is expected that certain winter-active species might disperse from one location along the gradient to another, perhaps to escape predators, or find winter-refugia. This would, in turn, change the pattern of distribution of the selected taxa across these ecotones. Surprisingly, the general pattern of distribution across these ecotones changed little. However, there were significant differences between summer, spring, winter and autumn catch, and species identities changed from one season to the next. For example, carabid abundance and species richness was higher in the forest, compared to in the grassland, while ants were species richer in the grassland, compared to in the forest. These patterns were consistent from one season to the next. Again, as was found in chapter II, *T. africana* was significantly more abundant at the ecotone, compared to either forest or grassland interiors, in all seasons throughout the year. To summarise, amphipods favoured the ecotone environment, carabids the forests and ants the grasslands, throughout the year.

Finally, scientists have recently become aware of the importance of the matrix surrounding habitat patches, in the survival and occurrence of organisms in the habitat patch. I tested whether the quality of the matrix, as a function of human disturbance, has an influence on invertebrate occurrence and distribution patterns across Afromontane forest-grassland boundaries. Redgrass

(*Themeda triandra* Forssk.) dominated Afromontane grasslands are, and have been experiencing varying degrees of anthropogenic disturbance. Consequently, ecotones vary from being very abrupt (heavy disturbance in the matrix) to gradual (little disturbance in the matrix), although still sharp compared to most ecotones elsewhere. Level of grassland disturbance influenced amphipod, carabid and ant assemblage-structure across Afromontane ecotones (chapter IV). Results support the hypothesis that the dynamics of remnant areas are influenced by factors arising in the surrounding landscape. In particular, carabid assemblage-composition changed highly significantly from undisturbed to disturbed sites (this taxon was mainly captured from forests). Furthermore, only a single carabid individual was captured from 8 to 128 m into the grassland and only 14 *T. africana* individuals were captured from 2 m inside the forest to 128 m into the grassland of the most disturbed site. Clearly, matrix quality influenced not only the patterns of occurrence of organisms in the grassland matrix, but also at the ecotones and in the forest patches.

In conclusion, it is imperative to investigate a number of taxonomic groups in conservation ecology to give more reliable results, and thus conservation recommendations. Of course, not all taxa can be considered, and the selection of appropriate taxa still poses a problem, but a set of taxa that are considerably different biologically is a good start. Native Afromontane forest-grassland mosaics are in urgent need of conservation, as much of this habitat is subject to heavy anthropogenic disturbance such as human settlement, forestry, cattle grazing, agriculture, and frequent, out of season, fires. Unfortunately only 2% of this biome is protected in South Africa. Furthermore, matrix quality is important because it determines the survival rate of propagules moving between remnant patches of habitat, and therefore the success rate of such movements. Private land-owners own most of this grassland area in the Afromontane region, but no guidelines are available to them on how to protect this habitat. Throughout this thesis I emphasised the importance of protecting both native forest and the surrounding native grassland. A first initiative is simply to protect a zone of grassland around the forest patches, both in terms of less frequent burning regimes, and less, or no cattle grazing here. By doing so, a rich grassland ant fauna will be conserved, the grassland matrix quality will improve, and a rich carabid fauna, favouring predominantly Afromontane forest remnants, will be conserved.

CONTENTS

Chapter 1. General introduction

Landscape fragmentation

With an increasing loss of natural habitat, associated with population extirpation and a decrease in species richness, many studies in conservation biology have focused on habitat fragmentation, especially forest fragmentation (Harris, 1984; Wilcove *et al.*, 1986; Wilson, 1988; Sutton and Collins, 1991). Humans fragment the landscape (Noss, 1987; Matlack, 1993) with agricultural activities being a major factor responsible for loss of native habitat, and a major cause of decline in biodiversity (Majer *et al.*, 1997). Anthropogenic fragmentation is usually initiated by the building of roads into a natural landscape (dissection), followed by the conversion of natural ecosystems into agricultural lands (perforation), then the isolation of natural ecosystems by converting more land to agriculture (fragmentation), and finally by converting even more of the remaining natural patches, causing highly isolated natural patches (attrition) (Forman, 1995; Hunter, 1996). Anthropogenic fragmentation takes place over short periods of time, and, unlike natural fragmentation, is usually not associated with large-scale climatic changes (Naveh and Lieberman, 1990; Forman, 1995).

Fragmentation transforms large homogenous habitat into smaller homogenous units (Forman, 1995). These smaller remnant areas of native vegetation are isolated from one another in terms of fauna and flora (Wilcove *et al.*, 1986), and are surrounded by a matrix with a dissimilar community structure and organismic composition (Forman and Godron, 1981; Saunders *et al.*, 1991). Fragmentation thus causes habitat heterogeneity in the landscape (Jagomägi *et al.*, 1988), at both local and regional scales (Ricklefs, 1987).

In addition to decreasing patch-size and connectivity of the focal habitat, fragmentation also causes habitat loss. This effect is at least equally harmful to species restricted to the focal habitat than isolation of the remnants. However, it is often difficult to distinguish the effects of fragmentation (isolation effects, small size of fragments) from those caused by pure habitat loss (Haila, 1999).

Studies on fragmentation traditionally focus on habitat islands as units distributed in a 'hostile' matrix (Harris, 1984). These area-related studies measured patch size and correlated results with species number and structure within these patches (Doak and Mills, 1994). Effects of habitat edges were recognised, but usually not incorporated into many of these studies. Now, however, there is an awareness of the dynamic nature of the landscape, particularly the significance and function of habitat edges, whether they are inherent or induced (Yahner, 1988; Laurance, 1997).

Jagomägi *et al.* (1988) suggested that edges and not areas or habitat patches play the leading role in landscape ecology, while Naiman and DéCamps (1991) suggest that ecotones are key landscape elements. Furthermore, the more spatially heterogeneous a landscape, the greater is the boundary area between any given landscape element (Simberloff and Gotelli, 1984; Yahner, 1988). These boundary areas, or ecotones, form an integral part of the landscape (Churkina and Svirezhev, 1995; Kolasa and Zalewski, 1995; Laurance, 1997).

Ecotones

The term ecotone comes from the Greek words *oikos* (household) and *tonos* (tension). So it literally means 'tension zone' or transition area (Longman and Jeník, 1992) between adjacent communities (Harris, 1988; Angelstam, 1992). However, the ecotone concept is far more complex. It includes scaling, structural and functional aspects, and has spatial complexity and temporal dimensions (Kolasa and Zalewski, 1995). Holland and Risser (1991) defined an ecotone as '...a zone of transition between adjacent ecological systems, having characteristics uniquely defined by space and time scales and by the strength of the interactions between the adjacent ecological systems'. Ecological conditions change more rapidly in an ecotone than in adjacent areas leading to rapid changes in structure, function and composition of biota (Jagomägi *et al.*, 1988). Apart from unique characteristics, ecotones also have compositional and structural characteristics from both adjacent habitats (Risser, 1995).

Adejuwon and Adesina (1992) have identified three types of ecotones. In the first type two contrasting communities compete for space at their point of junction. Here no intermediates are produced and the edge of either community is continually advancing or retreating. The second is a transitional vegetation where the ecotone is a combination of species and characteristics from both adjacent communities. The third type is where the ecotone has its own unique vegetation (Fig. 1).

So, ecotones can vary from being gradual and wide to abrupt (DéCamps *et al.*, 1990; Longman and Jeník, 1992) (Fig. 1). In gradual ecotones, the overlap zone may not be easily distinguishable from the adjacent landscape elements (Forman and Godron, 1986) (Fig. 1). This makes biome demarcation difficult. Ecotones usually become more abrupt with an increase in disturbance (Forman and Godron, 1981), or when the main environmental factor is present on only one side of the boundary (Báckeus, 1993). These abrupt ecotones, or habitat edges, are major, even dominant features of heavily fragmented landscapes. Edge effects, the physical and biological changes associated with fragment margins (Murcia, 1995), are of principal importance at these abrupt ecotones (Laurance, 1997).

Recently, Smith *et al.* (1997) argued that

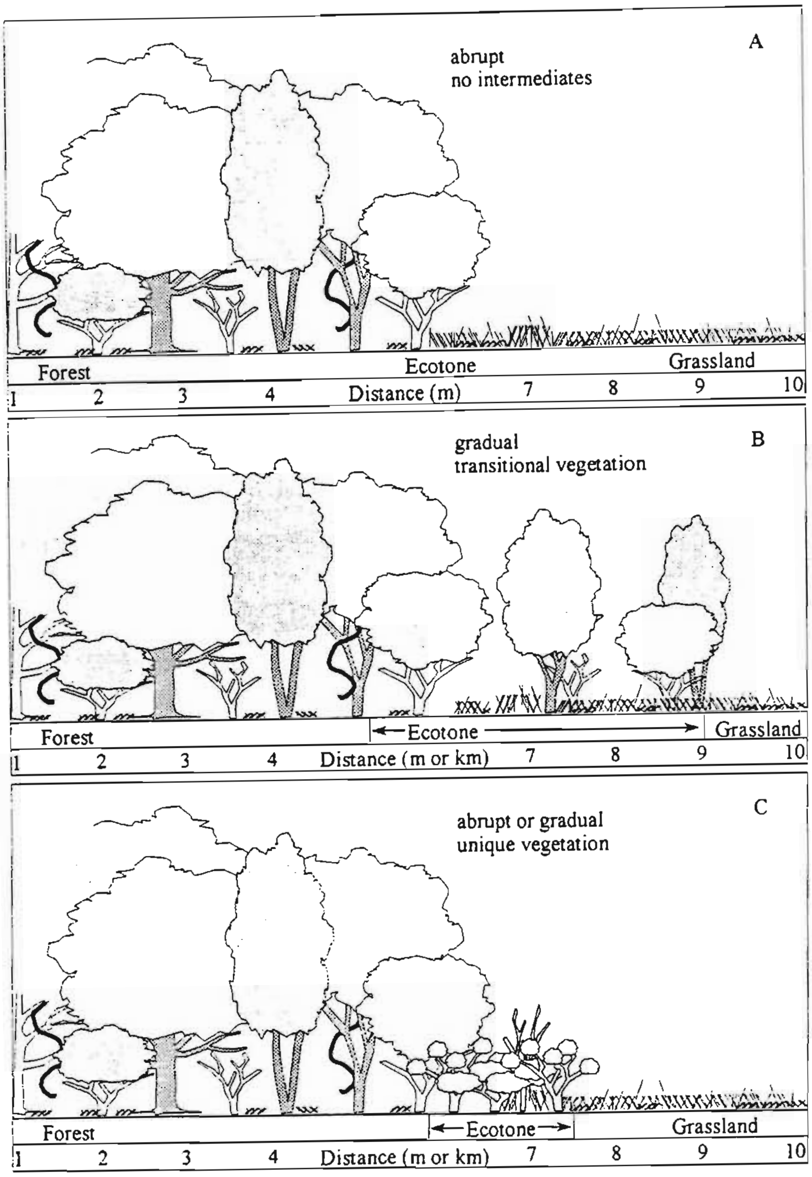

Fig. 1. Ecotone types between forest patches and a grassland matrix. **A** - an abrupt ecotone where no transition area is visible, **B** - a gradual ecotone where vegetation from both biotopes constitutes the transition area, **C** - an ecotone where the vegetation differs from those of the adjacent biotopes.

geographically large ecotones, like the African rainforest-savanna transition, may be a source of evolutionary novelty. They suggest that these ecotones may be integral to the production and maintenance of biodiversity in tropical rainforests, confirming the suggestion by Longman and Jeník (1992) that the evolution of life forms has often been associated with interfaces between contrasting environments.

Edge effects

Edge effects are a main characteristic of ecotones, although not all ecotones exhibit edge effects (Forman, 1995). Murcia (1995) identified three types of edge effects: abiotic, direct biological and indirect biological. Abiotic effects involve changes in environmental conditions that result from proximity to a structurally dissimilar matrix. Direct biological edge effects involve changes in the distribution and abundance of species caused by the physical conditions near the edge. Indirect biological edge effects result from changes in species interactions at or near the edge.

Direct biological edge effects

The classical edge effect definition hypothesises an increase in variety and diversity at community junctions, thus an increase in biological diversity across an ecotone (Leopold, 1933; Kroodsma, 1982; DéCamps *et al.*, 1990; Holland and Risser, 1991; Bedford and Usher, 1994), or simply the accumulation of life at ecotones (Jagomägi *et al.*, 1988). The greater the ratio of density at an edge to density in the community interior, the greater the edge effect (Kroodsma, 1984).

An edge species performs all or most of its activities at or near the edge, while interior species are active away from the edge (Yahner, 1988). The practicality of identifying edge effects, however, poses problems. Yahner (1988) identified these as; 1) time spent at edges varies among species; 2) intraspecific use of an edge varies with season; and 3) intraspecific use of an edge varies among geographic regions. It is not surprising that there is little consensus on the significance of edge effect results. This lack of agreement can be in part contributed to poor experimental design, insufficient knowledge on ecotone mechanisms, and the site specificity of species occurrences with no generalised, universal theory (Murcia, 1995).

Nevertheless, a number of studies concur that biological edge effects do occur in certain birds (Kroodsma, 1982; Lovejoy *et al.*, 1986; Cavalcanti, 1992), plants (Simberloff and Gotelli, 1984; Barbour *et al.*, 1990; Turton and Duff, 1992; De Casenave *et al.*, 1995), mammals (Sekgororoane and Dilworth, 1995; Holmes, 1996) and invertebrates (Webb and Hopkins, 1984; Helle and Muona, 1985; Lovejoy *et al.*, 1986; Webb, 1989; Raw, 1992; Burkey, 1993; Bedford and Usher, 1994; Downie *et al.*, 1996; Magura and Tóthmérész, 1997). But, as Didham (1997a) emphasised, this increase in species richness at the edge is almost certainly due to the invasion of generalist species from disturbed habitats outside forest fragments (see also Halme and Niemelä, 1993; Usher *et al.*, 1993).

Edge effects do not always occur at habitat junctions. Heske (1995) found no edge effects in small mammal abundance between forest edges and interiors. Similarly, Spence *et al.* (1996) found no edge effects for carabids in boreal forests. A negative edge effect on the composition and density of testacean communities in a meadow-spruce forest mesoecotone was found (Balík, 1996), while Van der Merwe *et al.* (1996) showed that ground-living spider richness was lowest at an indigenous forest-pine plantation ecotone. Quality of edges may vary considerably for different kinds of wildlife and consequently the edge effect hypothesis is not universal.

Abiotic edge effects

Abiotic edge effects, the change in environmental conditions that result from proximity to a structurally different matrix (Murcia, 1995), are present at almost all human-created forest fragments. Microclimatic characteristics at forest edges are less well understood (McNaughton, 1989). Nevertheless, solar radiation and wind movement are perhaps the main meteorological factors influencing abiotic conditions at habitat edges, with Forman and Baudry (1984) arguing that wind is the driving force controlling other environmental variables at habitat edges. These environmental variables include, among others, soil moisture, relative humidity and temperature, and usually change significantly from habitat interior to edge. For example, Laurance (1991) showed that soil moisture decreased, while temperature variation increased at forest edges. Similarly, Williams-Linera (1990) illustrated that the greatest changes in temperature and relative humidity occurred between 2.5 m and 15 m into forests in Panama. More recently, Kapos *et al.* (1997) showed that at newly exposed edges, vapour pressure deficit increased at least 60 m into a 100 ha Brazilian forest fragment, while Stevens and Husband (1998) illustrated that relative humidity decreased while air and soil temperatures increased significantly at two Atlantic forest fragment edges.

Distances up to which abiotic edge effects penetrate forest fragments differ considerably between, and within, habitat types. Extremes, for example, include changes in abiotic conditions from as little as 2.5 m into forest fragments (see above), to up to 200 to 500 m into fragments from the edge (Laurance, 1991), which also depend on edge orientation (Louda *et al.*, 1987; Bedford and Usher, 1994). Some of these clear-cut edge effects are related to time, where modifications disappear or become more complex as the edge ages (Angelstam, 1992; Matlack, 1993; Kapos *et al.*, 1997). Nevertheless, the deeper these environmental effects penetrate a habitat patch, the larger the patch has to be to support interior conditions (Lovejoy *et al.*, 1986).

Solar radiation and wind also change the structural characteristics of habitat edges (Angelstam, 1992), which in turn influence both biological and abiotic edge effects. For example, wind increased density of dead trees at edges (Williams-Linera, 1990; Young and Mitchell, 1994), while increased sunlight stimulates vegetation growth at edges (Lovejoy *et al.*, 1986). Therefore, edges often have a higher vegetation biomass than interiors (Williams-Linera, 1990; Burkey, 1993; Puyravaud *et al.*, 1994; Young and Mitchell, 1994), increasing structural heterogeneity, and consequently more niche space for invertebrates in particular.

Apart from sunshine and wind movement, fire can also have a significant effect on environmental conditions and vegetation structure (Everard, 1986; Hopkins, 1992; Jones, 1992; Puyravaud *et al.*, 1994; Schwartz *et al.*, 1996) at habitat edges. For instance, fire can increase tree mortality (Moll, 1976; Turner and Corlett, 1996) and stimulate vegetation growth (Lovejoy *et al.*, 1986) at forest edges.

Indirect biological edge effects

The strength of interspecific interactions differs at habitat edges from those in the interiors. For example, bird nest predation and nest parasitism increased at edges (Noss, 1987; Andrén and Angelstam, 1988; Harris, 1988; Small and Hunter, 1988; Møller, 1989). During unfavourable events in the surrounding habitat, predators seek cover at habitat margins (Clark and Gilbert, 1982; Maelfait and De Keer, 1990). Margins also provide overwintering sites for some organisms (Bedford and Usher, 1994), while others use them for migration (Risser, 1995). Consequently, edges appear to be habitats where predation is high. Edges appear attractive in terms of occupancy, but are costly in terms of low reproductive output and lower survival rates (Mazurkiewicz and Rajska-Jurgiel, 1987; Harris, 1988; Yahner, 1988).

Setting the scene: the Afromontane forest-grassland landscape

For several reasons South African Afromontane forest-grassland mosaics provide an excellent opportunity to study ecotone characteristics, and the possible effects of matrix quality on species assemblages within the forests. Firstly, these forest-grassland ecotones are naturally sharp, a consequence of both an almost annual burning regime in the grassland matrix and the frequent occurrence of natural fire in the region (Fig. 2). Unlike many forest fragmentation studies, where the edge studied is a consequence of clear-cutting of forest to give way to agriculture, edges in the Afromontane region are between vegetation types that have been in existence for, perhaps, millions of years (Lawes, 1990; Eeley *et al.*, 1999). Thus forest-grassland mosaics in the Afromontane region provide a good opportunity to study physical and biological changes across natural ecotones, where contrasting habitats lie side by side.

Secondly, although naturally sharp, recent human activity in the Afromontane region has increased the sharpness of some of the ecotones (transition from forest to grassland can happen within a metre). This provides an ideal opportunity to study possible changes in ecotone characteristics from a naturally-sharp to anthropogenically-sharp situation, and the possible effects of matrix disturbance regimes on invertebrates at edges and in forest remnants.

Most fragmentation studies often do not consider the quality of the areas surrounding remaining habitat, the matrix. Matrix

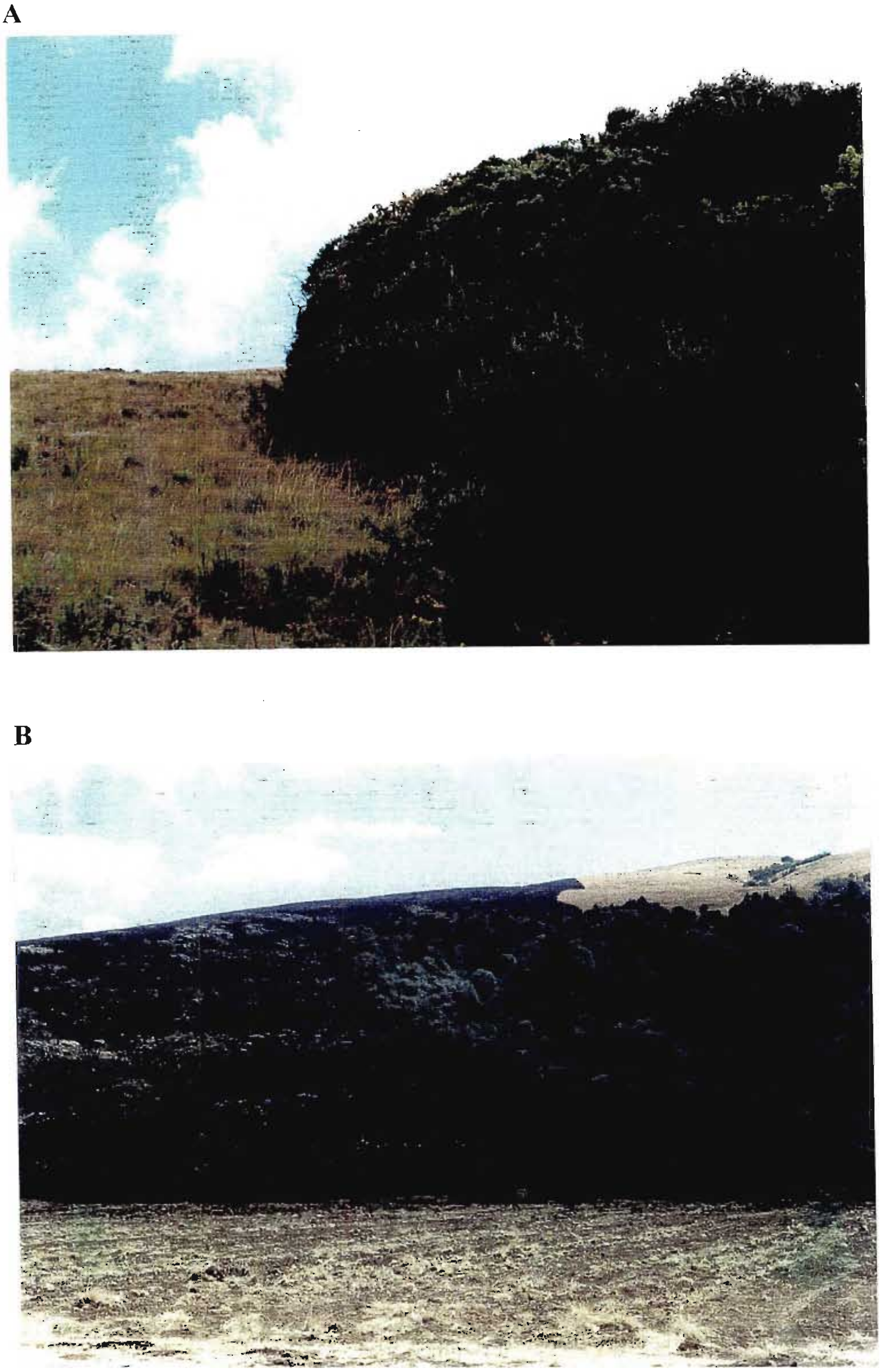

Fig. 2. **A** - Sharp transition between an Afromontane forest patch and the surrounding grassland matrix, **B** - Fire damage in the Afromontane grassland matrix.

characteristics are important because they determine the survival rate of individuals moving between remnant patches of habitat (Fahrig, 1999). At the landscape scale, matrix quality can have a significant effect on the survival probability of the regional population. Saunders *et al.* (1991) hypothesised that the dynamics of organisms in habitat patches are somehow driven by factors arising in the surrounding landscape, in other words, matrix characteristics, or matrix quality matters (Forman, 1995; Fahrig, 1999). In the Afromontane system, matrix quality may be of considerable importance for the continual survival of species in the isolated Afromontane forest complex.

And thirdly, to date, no conservation protocol is available for this Afromontane region. Fortunately, land-owners generally see native forest remnants as an asset, and little disturbance takes place in these forests. Native grasslands, however, are considered of little conservation value. This is surprising since Afromontane grasslands are rich in regional endemics, while the tree flora of the patches of undifferentiated evergreen Afromontane forests are endemic poor (Matthews *et al.*, 1993). Grasslands are transformed by agricultural and forestry practices, and settlement, while some grasslands are burnt on an almost annual basis (Fig. 2) to provide new growth for cattle grazing. Fires do not usually penetrate Afromontane forests, but do contribute significantly to the sharp transition observed between forest and grassland, in preventing the growth of marginal scrub (Lawes and Eeley, 2000) and in limiting the extent of forest patches, both locally and regionally (Eeley *et al.*, 1999).

Invertebrates as study organisms

Didham (1997b) points out that there are relatively few published works dealing with the effects of forest fragmentation on invertebrates, but argues that there is generally an increase in abundance and diversity of invertebrates at forest edges (Didham, 1997a).

Although little is known about distribution and diversity patterns of invertebrates in the Afromontane region, their potential for signalling effects of fragmentation are immense. Invertebrates are small, 'hyperdiverse', sensitive to environmental variability, good indicators of habitat heterogeneity, species diversity, and environmental stress, and their function in ecosystems is indisputable (Erwin, 1982; Stork, 1988; Dempster, 1991; Wilson, 1992; Niemelä *et al.*, 1993; Stork, 1993; Colwell and Coddington, 1994; Hill, 1995; Weaver, 1995; McGeoch, 1998). A reduced set of epigaeic invertebrates was chosen as study subjects because; 1) high invertebrate species richness makes it impossible to sample the entire fauna adequately, 2) invertebrates are insufficiently known taxonomically (acutely so in the Afromontane region), and 3) the subset selected here have been used as indicators in many studies (Stork, 1988; Brown, 1991; Kremen *et al.*, 1993; New, 1993; Colwell and Coddington, 1994; Margules *et al.*, 1994; Giller, 1996; Niemelä, 1996; Andersen, 1997). Taxa selected included terrestrial amphipods (with a single species present in the Afromontane region; *Talistroides africana* Griff.), and epigaeic carabids and ants (in chapter I, epigaeic spiders and rove-beetles were also included).

The term assemblage was used throughout the study to delineate these phylogenetically related invertebrate groups (Fauth *et al.*, 1996) within the spatially restricted forest-grassland community.

Hypotheses and thesis layout

This community-based thesis attempts to integrate various concepts of ecology, i.e. landscape ecology, indicator organism selection, habitat fragmentation, species diversity and conservation. Evidence suggests that edge effects occur mainly at anthropogenically-created habitat junctions. These human-created edges show significant differences in environmental conditions across them (see above), and often have a high species richness, a result of new vegetation growth at these edges and invasions of generalist species from the disturbed surrounding landscape (Didham 1997a). However, as these clear-cut edges mature and modifications disappear or become more complex, edge effects seem to become less pronounced (Kapos *et al.*, 1997). If it is assumed that mature clear-cut edges are, in fact, natural habitat edges, I hypothesise that natural Afromontane forest-grassland ecotones do not show biological or abiotic edge effects. Afromontane forest-grassland boundaries are sharp, but are not a result of forest clear-cutting. Rather, Afromontane forest-grassland boundaries are mainly fire maintained, and have been in existence for perhaps millions of years (Lawes, 1990).

To test this hypothesis, the following procedure was followed. In chapter I, the multi-taxa hypothesis was tested. Here, the diversity patterns of four epigaeic invertebrate groups (spiders, carabids, staphylinids and ants) were compared in five naturally-fragmented Afromontane forest remnants. Throughout this thesis the importance of a multi-taxa approach in conservation-related issues is emphasised. Different invertebrate taxa respond differently to environmental alterations, which is in itself an obvious statement, but nevertheless needs to be considered in conservation considerations. Using a subset of taxa selected in chapter I, the edge effect hypothesis was tested in chapters II and III. In chapter II, the distribution patterns of carabid and ant assemblages across six Afromontane forest-grassland ecotones were investigated to test whether biological edge effects do occur across natural habitat boundaries. In chapter III, inter-seasonal variation of these two taxa across a single ecotone was examined, to establish whether or not assemblage patterns change from one season to the next. In chapter IV, the effects of different grassland matrix disturbance-regimes on the distribution patterns of carabid and ant assemblages across five Afromontane forest-grassland ecotones were evaluated.

A further objective of the present study was to provide guidelines to land-owners on why, and how they should conserve these natural Afromontane forests and, importantly, the grasslands.

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Support for the multi-taxa approach in biodiversity assessment, as shown by epigaeic invertebrates in an Afromontane forest archipelago

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Often a single indicator invertebrate taxon is used for assessing changing landscape patterns. However, we argue here against the exclusive selection of a single group. Covariation in diversity patterns of spiders, carabids, staphylinids and ants were compared in and between five highly naturally-fragmented Afromontane forest patches (size range: 3.5–25.2 ha) in South Africa. Significantly fewer individuals and species were captured in smaller forest patches (< 6 ha) for most of the taxa, except Formicidae, where a higher number of species were captured in medium-sized patches (7–9 ha). When sampling effort was standardized, a higher diversity (rarefaction and Simpson's diversity index) was obtained in the smaller patches for Carabidae, Staphylinidae and Formicidae. The only significant positive correlation between taxa, in terms of numbers of species, was between Carabidae and Staphylinidae. The other taxa showed only weak positive correlations between species richness, or negative correlations. Multivariate techniques showed significant species turnover between patch assemblages for each taxon, and also showed that some taxa are more similar in assemblage-structure than others. An index of complementarity showed that species compositions of the selected taxa varied greatly between forest patches of different sizes. Our results support the multi-taxa approach, in conservation studies, even at the level of taxonomically-related groups sharing a common habitat stratum.

Keywords: Afromontane forests, epigaeic invertebrates, biodiversity assessment, multi-taxa approach.

Introduction

Choosing a group of organisms as an indicator for making decisions for the preservation of biological diversity is a fundamental task (Landres *et al.*, 1988). Brown (1991) suggested that the ideal group will facilitate many aspects of a conservation programme, from the initial identification of sites 'worthy' of conservation, public awareness, continuous monitoring and management, to the predictive value of other sites. Furthermore, indicator groups should have already attracted much attention, should be taxonomically well-known, easy to collect, and be reasonably diverse (Sutton and Collins, 1991).

Invertebrates are useful in conservation studies because they are sensitive to environmental changes and will thus signal human-caused disturbances (Desender *et al.*, 1991). However, the sorting of such a vast array of often unidentifiable invertebrate species is a formidable task (Kremen *et al.*, 1993; Samways, 1994). Therefore, conservationists and managers have often opted for selecting a taxonomically well-known indicator group, or more precisely, biodiversity indicator group (McGeoch, 1998), in the hope that this group will positively reflect the patterns and processes of biological diversity in the landscape. Shortcomings in selecting a single taxon as a diversity estimate of others are various. For example, it is assumed that the variation in diversity in the indicator group correlates with that of the unrepresented groups (Colwell and Coddington, 1994; Reid, 1998). Although this may be true in some cases, recent work has suggested that diversity patterns vary widely between taxa, and that management programmes based on the knowledge of a single taxon would not necessarily predict or safeguard the diversity of others (Prendergast *et al.*, 1993; Báldi and Kisbenedek, 1994; Lawton *et al.*, 1998; Niemelä and Baur, 1998; Oliver *et al.*, 1998; Reid, 1998). These studies correlated diversity characteristics of a suite of organisms from phylogenetically distant groups in different habitat types, e.g. birds, beetles, butterflies, canopy invertebrates, soil and epigaeic invertebrate fauna, vertebrates

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and vegetation. There were differences in diversity among these groups, for example, they occupied distinctly different habitat strata.

Another approach to testing the value of single taxon indicators would be the study of indicator properties of a suite of more closely-related groups, both in terms of taxonomy and niche occupancy. Epigaeic invertebrates are most appropriate in multi-taxa conservation-oriented research for several reasons: (1) they include two of the most-studied terrestrial taxa (Carabidae and Formicidae); (2) they are associated with one of the most complex habitat systems, i.e. the soil (Stork and Eggleton, 1992; Giller, 1996); and (3) they are easily captured using standard techniques, one of which is pitfall trapping. Oliver and Beattie (1996) used a suite of epigaeic invertebrates, i.e. ants, beetles and spiders in biodiversity assessments in Australian temperate hardwoods, and argued for the need for similar studies in different environments.

The aim of this study is fourfold. First, to estimate the diversity of four *a priori* selected taxa (Araneae, Carabidae, Staphylinidae, Formicidae, whilst providing abundance data on one species of a very abundant amphipod *Talistroides africana*, Griff.), in a natural Afromontane forest-patch archipelago in South Africa. Secondly, to appraise critically whether one of these epigaeic invertebrate taxa can be used as a surrogate for biodiversity (McGeoch, 1998) of the other three groups. Thirdly, to consider whether a combination of taxa gives a more realistic picture of local biodiversity. And finally, to examine changes in the diversity of these groups with forest fragmentation.

Sites, materials and methods

Study area

Five forest patches (size range: 3–25 ha) were identified on the farm Nhlosane, Impendle (29°35′S 29°58′E) in the KwaZulu-Natal midlands, South Africa (Fig. 1). Patches were surrounded by *Themeda triandra* Forssk.

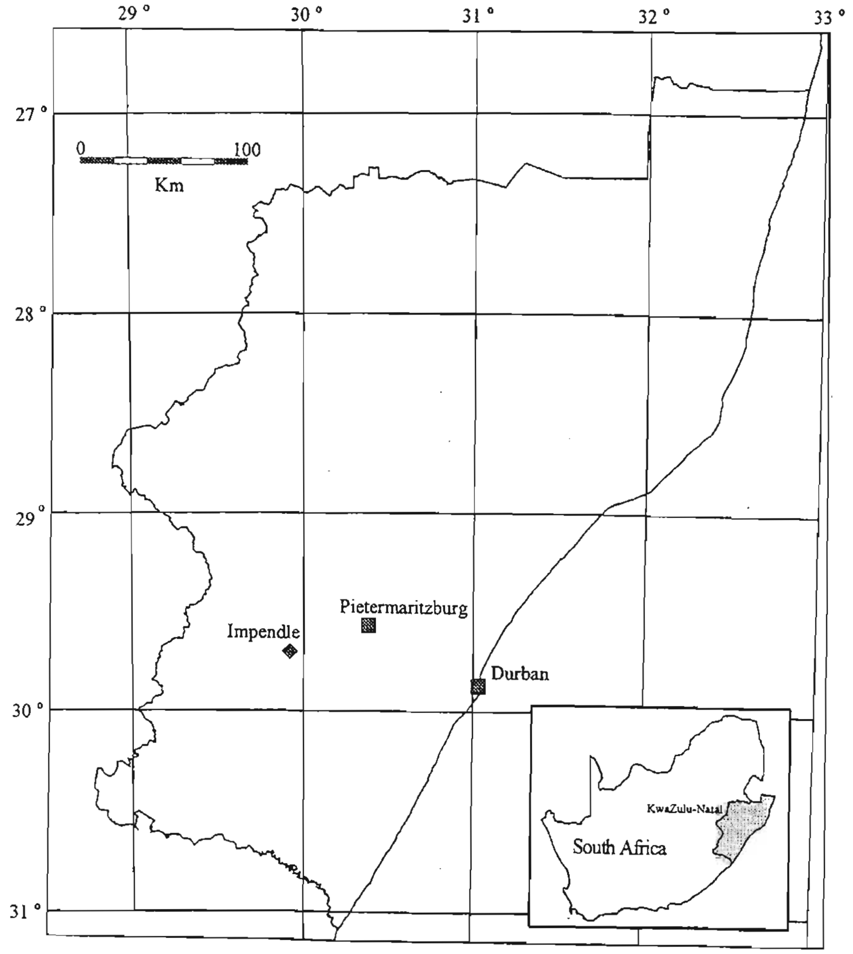

Figure 1. Location of the study area, Impendle, in the KwaZulu-Natal province, South Africa.

dominated grassland, which is mostly subject to deliberate annual burning, which simulates natural burns. Grassland fires do not normally penetrate these coarse-grained *Podocarpus* forest patches (Everard *et al.*, 1994, 1995). Forest patches were within 5 km of each other, on south-facing hill slopes at an altitude of 1800 m a.s.l. These five forest patches were divided into three size classes for reasons of simplicity: small (3.5 ha and 5.3 ha), medium (7.4 ha and 8.7 ha) and large (25.2 ha).

Sampling design and epigaeic invertebrate taxa captured

Epigaeic invertebrates were captured using pitfall traps. Glass tubes (25 mm wide, 150 mm deep) containing ± 20 mm of 70% ethyl alcohol and glycerol (3:1), were placed flush with ground level (Majer, 1978). Transects were laid out by placing a 10 m line of three replicate traps (5 m apart) at the forest edge, and then at 1 m, 2 m, 4 m, 8 m, 16 m, 32 m and 64 m into the forest. Each transect-set was therefore made up of 24 pitfall traps (8 × 3). This $\log_2$ layout was chosen to fine-sample the forest edge, and also provide information reasonably deep into the forest (Williams-Linera, 1990; Laurance 1991; Burkey, 1993; Didham, 1997). Patches that were too small to have a trap placed exactly at 64 m (i.e. the patch had a diameter of less than 128 m), had a trap placed as close as possible to the centre of the forest patch. Forest size affected how many sets of transects were possible. This meant that the three smallest patches (patch numbers 1, 2 and 3) had one transect-set of 24 traps each, patch number 4 had two sets and patch number 5, the largest one, had five sets, making the total number of traps 240. Transect-sets in patches 4 and 5 were placed 100 m apart to ensure, as far as possible, independent sampling (Digweed *et al.*, 1995). All transect-sets were placed on the western side of the patches. Traps were left in the field for two weeks prior to initial trapping, to reduce digging-in effects (Greenslade, 1973; Digweed *et al.*, 1995). Traps were removed and replaced every 14 days from the beginning of October 1993 until the end of December 1993. When rain flooded the traps, they were serviced before the 14 days were up.

Epigaeic invertebrate taxa sampled were landhoppers (Amphipoda), spiders (Araneae), ground beetles (Carabidae), rove beetles (Staphylinidae), and ants (Formicidae). Only a single landhopper species, *Talistroides africana* (Griff.), occurs in the Afromontane region, but its numbers and biomass are substantial. Spiders were identified to family, then to morphospecies. Ground beetles and ants, where possible, were identified to species, while rove beetles could only be identified to morphospecies (Oliver and Beattie, 1993, 1996; Beattie and Oliver, 1994, 1995). Although the morphospecies approach is not ideal in some circumstances (Brower, 1995; Campbell, 1995), the invertebrate fauna of the South African Afromontane complex is so poorly known taxonomically, that mostly only morphospecies could be used here.

Statistical analyses

A species accumulation curve was constructed for each of the four major epigaeic invertebrate taxa (excluding the monospecific Amphipoda). Sample order was randomized 100 times to eliminate sampling error and heterogeneity among the units sampled, and the mean and standard deviation of $S(n)$ (the number of species discovered) computed for each value of n between 1 and 240 (Colwell and Coddington, 1994). In comparing species richness among patch size-classes, we further adjusted the data to compensate for varying sample sizes. This was done by rarefaction, a statistical method for estimating the number of species expected in a random sub-sample drawn from a larger sample (Simberloff, 1978; Magurran, 1988) using the BIODIV (Baev and Penev, 1995) software.

A two-level nested ANOVA, with unequal sample size, was used to test for differences among patch size-class means. Our primary interest was in the variation among patch sizes in terms of abundances and species richness (for each taxonomic group selected) and secondly, in differences explained by the variation between traps placed at different distances from the forest edge. Although ant abundances at a site can reflect local bias as a consequence of their social existence (Hölldobler and Wilson, 1990; New *et al.*, 1996), no abnormally high abundance incidences were observed in the raw data matrices. Therefore, transformation of ant data to abundance classes was not necessary. All ANOVA data were transformed to approximate normality to comply with parametric assumptions (Clarke and Warwick, 1994; Sokal and Rohlf, 1995). The Scheffé unplanned comparisons test was used to investigate differences among means, resulting from the ANOVAs (Sokal and Rohlf, 1995). In addition, Simpson's diversity index was calculated for each patch size-class. This index reflects the probability that any two individuals drawn at random from a population will belong to the same species (Ludwig and Reynolds, 1988), and an increase in the reciprocal form (1/D) reflects increase in diversity (New *et al.*, 1996).

Assemblage-structure differences between the small, medium and large patches, and the different taxa selected, were compared using multivariate techniques. Non-metric multidimensional scaling (NMDS), calculated from a Bray-Curtis similarity matrix, was used to construct a map of the samples in two dimensions (Clarke and Ainsworth, 1993). Fourth-root transformations, which down-weight the effect of abundant species, were performed on the data. To test for differences in invertebrate assemblage-structure between samples, or as here patch size-classes, Clarke (1993) devised an analysis of similarity test, ANOSIM, on a simple non-parametric permutation procedure. ANOSIM uses the rank similarity matrix underlying the ordination or classification of samples (Clarke and Green, 1988).

In addition to the graphical representation of distinctness between patch-classes, paired similarity and complementarity were calculated. Similarity was calculated using the Bray-Curtis similarity index:

$$S_{jk} = 100\ \left(1 - \frac{\sum_{i=1}^{p} |Y_{ij} - Y_{ik}|}{\sum_{i=1}^{p} (Y_{ij} + Y_{ik})}\right)$$

where Y_{ij} and Y_{ik} are the abundance values for the i^{th} species in patch-classes j and k ($i = 1,2,\ldots,p$; j and $k = 1,2,\ldots,n$). Similarity values vary from 100% (total similarity) to 0% (total dissimilarity) (Clarke and Warwick, 1994). Complementarity was calculated using the formula:

$$C_{jk} = 100\ \left(\frac{\sum_{i=1}^{Sjk} |X_{ij} - X_{ik}|}{\sum_{i=1}^{p} \max(X_{ij}, X_{ik})}\right)$$

where X_{ij} and X_{ik} are the presence/absence values for the i^{th} species in patch-classes j and k. Complementarity values range between 100% (no species shared) and 0% (identical species lists) (Colwell and Coddington, 1994).

To complete the 'distinctness analysis' between patches, individual species mainly responsible for patch distinctness (i.e. contributions of each species to the dissimilarity between paired patches) were identified using the test SIMPER, or similarity percentage, which is explained in Clarke (1993).

Results

Epigaeic invertebrate abundance and diversity

Trapping yielded 2675 landhopper (*T. africana*) individuals, 865 spider individuals in 34 species, 665 ground beetle individuals in nine species, 3001 rove beetle individuals in 16 species, and 1629 ant individuals in 19 species (see Appendix). The landhopper, *T. africana*, was the most abundant species captured in this study. The most abundant spider species was Araneae sp. 4, representing 21% of total spider abundance, while the most numerous carabid species was Pterostichinae sp. 2, representing 77% of total carabid abundance. For staphylinids, the most abundant species was Staphylinidae sp. 10 representing 30% of total staphylinid abundance, while the most numerous ant species was *Crematogaster* sp. 1, representing 68% of total ant abundance (Fig. 2).

The lognormal distribution, which characterized species-abundance data of the four taxa selected, also estimates the unsampled species in the community, that is the species to the left of the veil line (Preston, 1962), with the following equation:

$$S^* = S/(1 - p_0),$$

where S^* is the total number of species in the community, S is the number of species sampled, and p_0 represents the area under the normal curve of the unsampled species (Magurran, 1988). The lognormal estimation of the number of Araneae species was 39, for Carabidae 11, for Staphylinidae 17, and for Formicidae 24.

The reliability of these estimates was confirmed by the shape of the species accumulation curves (Fig. 3). For example, the Araneae accumulation curve did not reach an asymptote after 240 samples and 34 species captured, but was estimated to reach a plateau at an estimated 39 species. The same pattern was observed for Formicidae (19 species captured, 24 estimated). On the other hand, the nine Carabidae species captured are close to the 11 estimated number of species, and this is reflected in the asymptotic structure of the Carabidae accumulation curve. This is also evident for the Staphylinidae accumulation curve (Fig. 3).

Rarefaction was used to calculate the number of species expected in each patch-class (Fig. 4), since sampling effort was unequal. Using the patch-class with the least number of individuals, the expected number of species, E(S), per class, per taxon, was calculated. For Carabidae and Formicidae, the largest forest patch had the lowest species estimation per standard number of individuals, while for Carabidae and Staphylinidae, the smallest patches estimated the largest number of species (Fig. 4).

Significantly different mean numbers of individuals for each taxon, except Araneae, were captured between patch-classes (Table 1). The highest mean number of individuals were captured in the largest forest for all

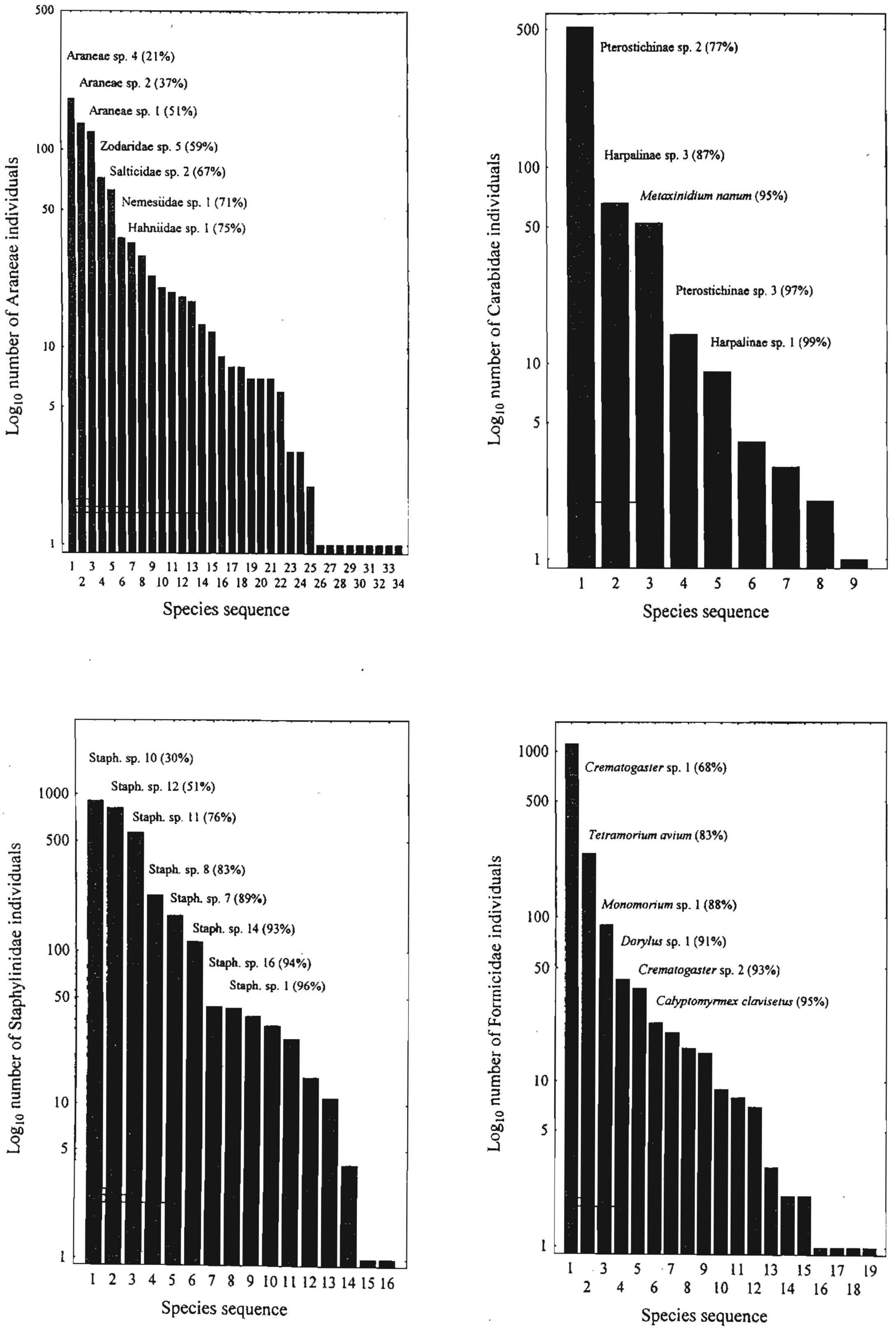

Figure 2. Rank abundance plots illustrating the abundance of each species on a logarithmic scale against the species' rank, in order from the most abundant to least abundant species. Species making up 50%, 75% and 90% of the total abundance are presented by the three horizontal lines, and the most abundant species (and their cumulative percentage contribution to total abundance) are given for Araneae, Carabidae, Staphylinidae and Formicidae.

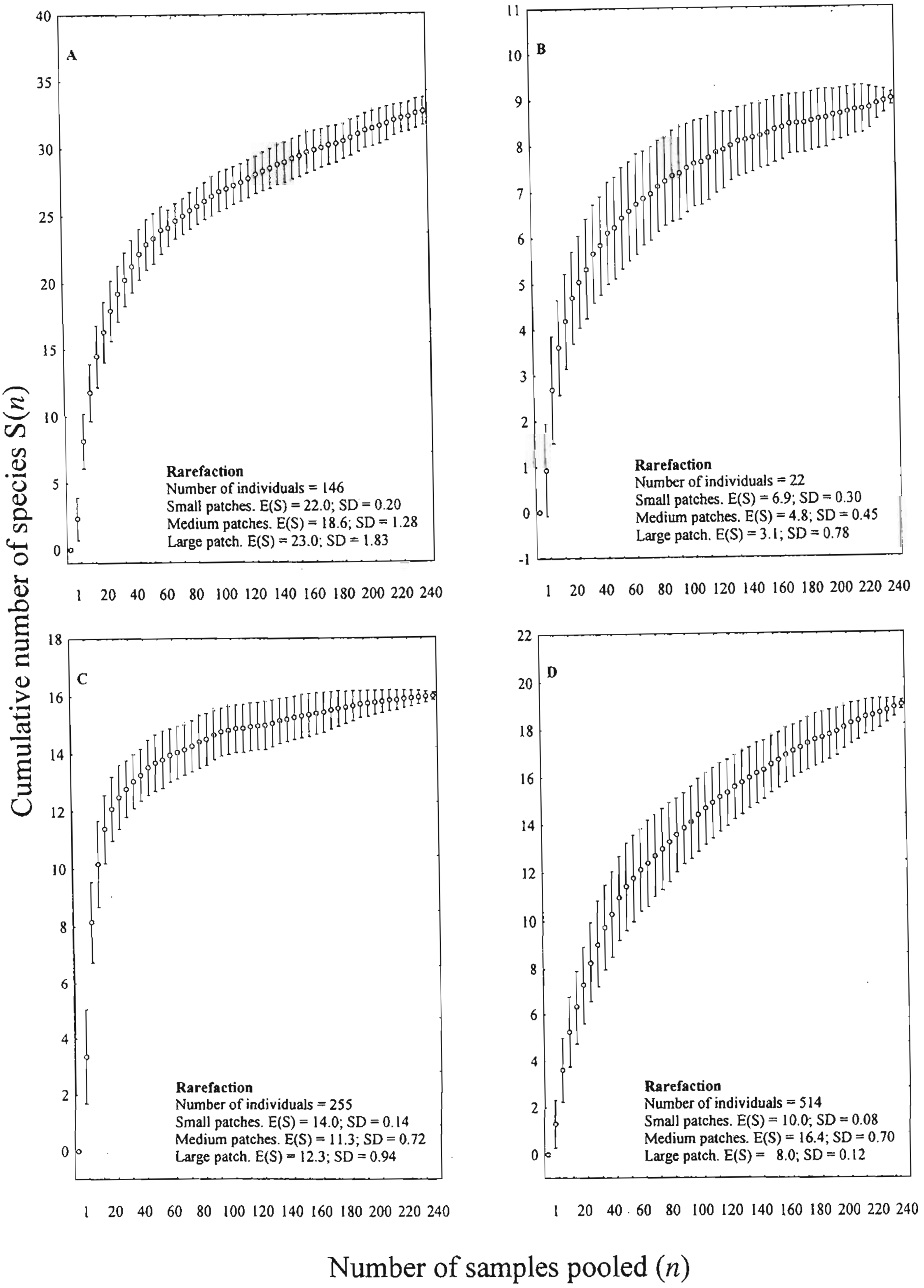

Figure 3. Species accumulation curves for the four taxa selected from 240 pitfall traps (A: Araneae, B: Carabidae, C: Staphylinidae, D: Formicidae). Each point represents the mean of 100 randomisations of sample pooling order. Error bars are the corresponding standard deviations. Fifty points are shown (after Colwell and Coddington, 1994). Rarefaction calculations are also shown. Expected number of species E(S), and standard deviations SD, were calculated on the patch size-class with the least number of individuals.

taxa, except Formicidae, for which a significantly higher mean number of individuals was captured in the small-sized patches (Fig. 4A). Species richness shadowed that of abundance (Table 1). Significantly higher numbers of species were captured in the largest patch, except for Formicidae where a significantly higher number of species was captured in the medium-sized patches (Fig. 4B). There were also distance effects, possibly a consequence of edge effects. This was evident for Amphipoda where more individuals were captured closer to the edge; for Staphylinidae where fewer individuals were captured closer to the edge; and Araneae where variable, but significantly different, numbers of species were captured from forest edge to forest interior (Table 1).

The similarity between abundance and species data is reflected in the relatedness between these two parameters. For each taxon, the number of species was

Table 1. Nested analysis of variance showing differences between mean numbers of individuals and species per patch size-class, and per distance from the forest edge (see Materials and methods), for Amphipoda, Araneae, Carabidae, Staphylinidae and Formicidae

Invertebrate group	Source of variation	df	Ms	F	p
*Individuals**					
Amphipoda	Among size-classes	2	1.358	3.943	0.035
	Among distances from the edge	21	0.344	2.504	0.003
	error	56	0.138		
Araneae	Among size-classes	2	0.619	2.199	0.136ns
	Among distances from the edge	21	0.282	1.851	0.035
	error	56	0.152		
Carabidae	Among size-classes	2	2.362	27.742	< 0.001
	Among distances from the edge	21	0.085	1.158	0.322ns
	error	56	0.074		
Staphylinidae	Among size-classes	2	19.169	10.086	< 0.001
	Among distances from the edge	21	1.901	1.970	0.023
	error	56	0.964		
Formicidae	Among size-classes	2	1.330	10.181	< 0.001
	Among distances from the edge	21	0.131	0.641	0.869ns
	error	56	0.204		
*Species**					
Araneae	Among size-classes	2	0.824	6.543	0.006
	Among distances from the edge	21	0.126	1.813	0.040
	errror	56	0.069		
Carabidae	Among size-classes	2	3.919	20.029	< 0.001
	Among distances from the edge	21	0.196	1.321	0.202ns
	error	56	0.148		
Staphylinidae	Among size-classes	2	23.215	14.335	< 0.001
	Among distances from the edge	21	1.619	1.528	0.105ns
	error	56	1.060		
Formicidae	Among size-classes	2	5.390	6.782	0.005
	Among distances from the edge	21	0.795	1.490	0.119ns
	error	56	0.533		

*Data were transformed to approximate normality when necessary.

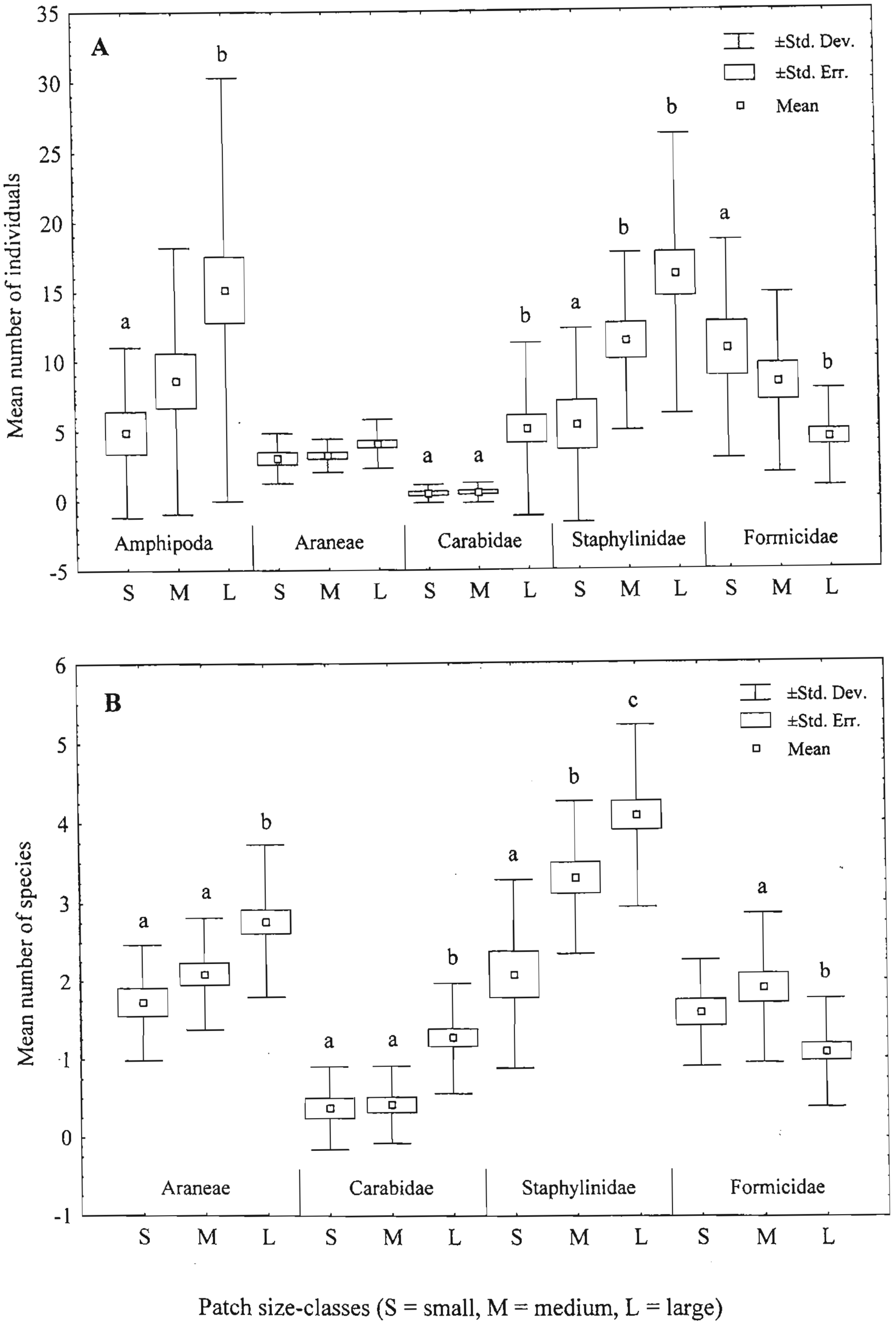

Figure 4. Mean numbers of individuals (A) and species (B) captured per patch size-class. Pairwise comparisons, within each taxon, show significant differences between means, where they exist (different letters within each taxon denote significant differences between means, at the 5% level).

Table 2. Simpson's index (given as I/D) for Araneae, Carabidae, Staphylinidae and Formicidae at small-, medium- and large-sized forest patches

Invertebrate taxon	Small patches (N = 2)		Medium patches (N = 3)		Large patch (N = 5)	
	Mean	SD	Mean	SD	Mean	SD
Araneae	4.75	0.97	6.42	4.42	9.96	1.46
Carabidae	5.56	0.09	3.83	0.55	1.48	0.30
Staphylinidae	5.04	0.39	3.83	0.65	4.36	0.56
Formicidae	2.01	1.05	2.36	0.69	1.58	0.49

The diversity indices were calculated on pooled transect-set data.

significantly correlated to the number of individuals captured: Araneae (Pearson correlation: $r = 0.74$, $df = 78$, $p < 0.001$), Carabidae (Pearson correlation: $r = 0.44$, $df = 78$, $p < 0.001$), Staphylinidae (Pearson correlation: $r = 0.65$, $df = 78$, $p < 0.001$) and Formicidae (Pearson correlation: $r = 0.43$, $df = 78$, $p < 0.001$). Furthermore, the number of Araneae species showed a weak positive correlation to the number of Carabidae species ($r = 0.16$, $df = 78$, $p = 0.89$ns), and to the number of Staphylinidae species ($r = 0.22$, $df = 78$, $p = 0.32$ns). The only significant positive correlation was between the number of Carabidae and Staphylinidae species ($r = 0.47$, $df = 78$, $p < 0.001$). Formicidae species richness did not correlate with Araneae ($r = -0.01$, $df = 78$, $p \sim 1.00$ns), and correlated negatively with Carabidae ($r = -0.29$, $df = 78$, $p = 0.06$ns), and Staphylinidae ($r = -0.20$, $df = 78$, $p = 0.50$ns). Bonferroni probabilities were calculated to correct for multiple correlations.

Simpson's diversity index (Table 2) indicated that Carabidae and Staphylinidae were most diverse in the smallest patches, while Araneae was most diverse in the largest patch. Formicidae was most diverse in the medium-sized patches.

Assemblage analysis

Assemblage ordination reduces the complexity of the high-dimensional community (Clarke and Warwick, 1994). Non-metric multidimensional scaling ordination showed some separation of patch sizes for Carabidae, Staphylinidae and Formicidae (Fig. 5). Araneae however, did not show clear separation. Nevertheless, all four taxa showed significant differences between patch sizes (p values in Fig. 5). Carabidae showed the clearest separation, and this is also evident in the high R statistic value. Carabidae is followed by Staphylinidae, Formicidae and then Araneae (Fig. 5). The significant differences in assemblages among patch sizes suggest similar levels of turnover between forest patch sizes.

Most of the patch sizes, per taxon, showed significant pairwise differences (Table 3), the only exception being between the small and medium patch sizes for Carabidae. Two points require mention here: (1) the higher stress values (a measure of how well the underlying relationship between samples are displayed in the ordination) in Araneae, Staphylinidae and Formicidae assemblage ordinations indicate lower confidence in the observed pattern; and (2) a lower scatter of points in the ordinations indicates greater assemblage similarity.

Overall similarity between the three patch size-classes were calculated using the Bray-Curtis similarity index (Table 4). Similarity between Araneae assemblages was highly consistent across patch size-classes. So too was that for Formicidae. Carabidae showed higher similarity among the small and medium patches than among small and large patches. Staphylinidae showed high similarity between patches, while Formicidae showed an overall lower similarity between patches.

Species presence/absence data were used to calculate complementarity (Table 4). The complementarity index showed that Staphylinidae shared most species among patches, while Formicidae shared the lowest number of species (highest percentage values). Both Araneae and Carabidae showed intermediate percentages. Small- and medium-sized patches shared the most species for all taxa, except for Staphylinidae, while medium- and large-sized patches shared the least, except for Staphylinidae and Formicidae.

Species contributing most to the dissimilarity observed between paired patch size-classes were identified, and the four 'best' discriminating species, per taxon, given (Table 5). For Carabidae, the four most abundant species (Fig. 2) were also consistently the best discriminators. For Formicidae, *Tetramorium avium*, the

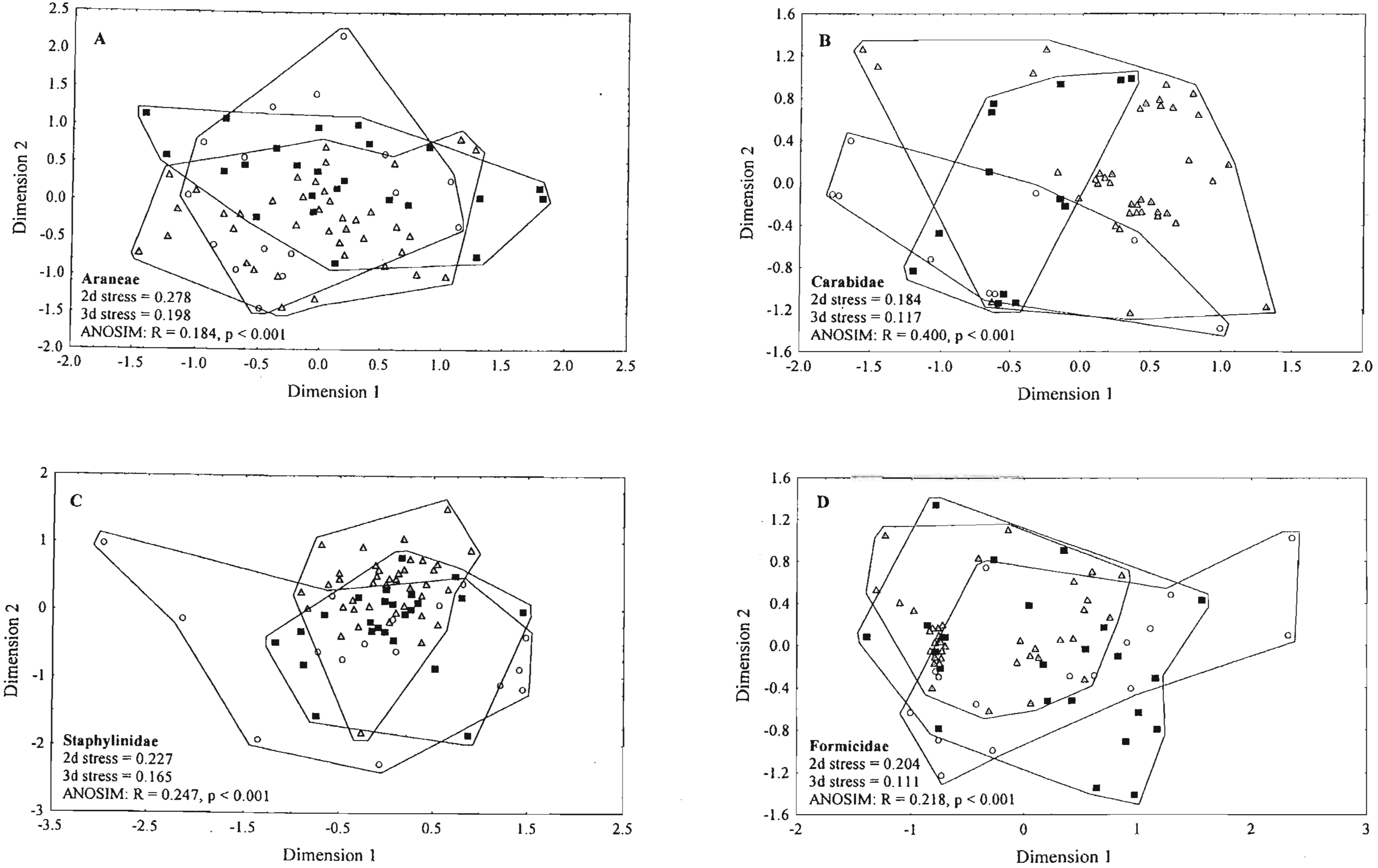

Figure 5. Non-metric multidimensional scaling ordinations for spiders, ground beetles, rove beetles, and ants. Symbol explanations: ○ = small patches; ■ = medium patches; ▲ = large patch. Stress values, ANOSIM R statistic and p values are also given.

Table 3. ANOSIM pairwise comparisons of patch size-classes (small, medium and large) using the Bray-Curtis similarity matrix, produced by Araneae, Carabidae, Staphylinidae, and Formicidae

	Comparisons*					
	Small and medium		Small and large		Medium and large	
Taxon	R	p	R	p	R	p
Araneae	0.159	0.002	0.216	0.001	0.169	< 0.001
Carabidae	0.116	0.07ns	0.525	< 0.001	0.353	< 0.001
Staphylinidae	0.176	0.003	0.484	< 0.001	0.105	0.013
Formicidae	0.096	0.03	0.294	< 0.001	0.201	< 0.001

*The significance levels in the pairwise tests are not adjusted to allow for multiple comparisons, prompting caution in interpretation of p-values close to 0.05

Table 4. Percentage values of Bray-Curtis similarity index, and complementarity index between the three patch size-classes (small, medium and large) for each epigaeic invertebrate taxon selected. Bray-Curtis data were $\sqrt{\sqrt{}}$-transformed to downweight the effect of common species, therefore taking account of rarer species. Complementarity index values were calculated on presence/absence data (values in parentheses represent numbers of species in common)

	Bray-Curtis similarity index			Complementarity index		
	Small	Medium	Large	Small	Medium	Large
Araneae						
Small	–			–		
Medium	75.1	–		34.6 (17)	–	
Large	69.9	70.4	–	37.5 (20)	40.6 (19)	–
Carabidae						
Small	–			–		
Medium	74.6	–		28.6 (5)	–	
Large	54.7	54.4	–	44.4 (5)	50.0 (4)	–
Staphylinidae						
Small	–			–		
Medium	78.9	–		26.7 (11)	–	
Large	71.8	82.2	–	18.8 (13)	20.0 (12)	–
Formicidae						
Small	–			–		
Medium	64.7	–		50.0 (9)	–	
Large	64.8	57.4	–	61.5 (5)	61.1 (7)	–

Higher Bray-Curtis index values represent a higher similarity between patch size-classes, while higher complementarity index values indicate lower complementarity between size-classes.

Table 5. Summary of dissimilarities between paired combinations of the three patch size-classes in terms of contributions from each species. Species are ordered in decreasing contribution ($\bar{\delta}i$), per taxon, and only good discriminating species ($\bar{\delta}i$/SD($\bar{\delta}i$)) are shown

Discriminating species between medium–small patches

Species name	$\bar{\delta}i$	SD($\bar{\delta}i$)	$\bar{\delta}i$/SD($\bar{\delta}i$)
Araneae			
Araneae sp. 2	5.55	4.08	1.36
Araneae sp. 1	3.25	2.78	1.17
Salticidae sp. 2	3.07	2.95	1.04
Hahniidae sp. 1	3.02	2.90	1.04
Carabidae			
Harpalinae sp. 3	12.92	13.18	0.98
Pterostichinae sp. 2	12.57	12.57	1.00
Pterostichinae sp. 3	12.25	12.89	0.95
Metaxinidium nanum	11.14	12.80	0.87
Staphylinidae			
Staphylinidae sp. 10	3.27	1.95	1.68
Staphylinidae sp. 7	2.74	2.36	1.16
Staphylinidae sp.12	1.91	1.27	1.50
Staphylinidae sp. 11	1.85	1.38	1.34
Formicidae			
Tetramorium avium	7.47	5.49	1.36
Crematogaster sp. 2	6.34	5.42	1.17
Monomorium sp. 1	5.86	5.01	1.17
Crematogaster sp. 1	4.41	4.05	1.09

Discriminating species between large–small patches

Species name	$\bar{\delta}i$	SD($\bar{\delta}i$)	$\bar{\delta}i$/SD($\bar{\delta}i$)
Araneae			
Araneae sp. 2	3.34	2.74	1.22
Nemesiidae sp. 1	3.13	2.50	1.25
Tetragnathidae sp. 1	2.71	2.22	1.22
Araneae sp. 4	1.78	1.27	1.40
Carabidae			
Pterostichinae sp. 2	22.27	7.95	2.80
Metaxinidium nanum	9.47	7.52	1.26
Harpalinae sp. 3	8.29	6.91	1.20
Pterostichinae sp. 3	6.66	6.80	0.98
Staphylinidae			
Staphylinidae sp. 6	3.83	1.60	2.40
Staphylinidae sp. 10	3.33	1.78	1.87
Staphylinidae sp. 1	3.17	2.09	1.52
Staphylinidae sp. 11	1.70	0.78	2.18
Formicidae			
Crematogaster sp. 2	10.08	6.63	1.52
Monomorium sp. 1	7.92	6.29	1.26
Tetramorium avium	7.91	5.14	1.54
Crematogaster sp. 1	6.17	4.94	1.25

Discriminating species between medium – large patches

Species name	$\bar{\delta}i$	SD($\bar{\delta}i$)	$\bar{\delta}i$/SD($\bar{\delta}i$)
Araneae			
Nemesiidae sp. 1	3.51	2.60	1.35
Linyphidae sp. 1	3.50	2.30	1.52
Salticidae sp. 2	3.03	2.35	1.29
Tetragnathidae sp. 1	2.71	2.22	1.22
Carabidae			
Pterostichinae sp. 2	20.16	11.20	1.80
Metaxinidium nanum	16.29	6.65	2.45
Harpalinae sp. 3	10.44	9.32	1.12
Pterostichinae sp. 3	6.29	7.23	0.87
Staphylinidae			
Staphylinidae sp. 13	2.82	2.14	1.32
Staphylinidae sp. 12	2.15	1.63	1.32
Staphylinidae sp. 7	1.63	0.96	1.69
Staphylinidae sp. 11	1.19	0.79	1.51
Formicidae			
Tetramorium avium	7.79	5.77	1.35
Monomorium sp. 1	6.08	5.68	1.07
Crematogaster sp. 1	4.22	3.30	1.28
Crematogaster sp. 2	3.55	3.90	0.91

Overall discriminating species

Species name	$\bar{\delta}i$	SD($\bar{\delta}i$)	$\bar{\delta}i$/SD($\bar{\delta}i$)
Small–medium			
Tetramorium avium	1.69	1.26	1.34
Araneae sp. 2	1.51	1.01	1.49
Talistroides africana	1.44	1.13	1.27
Crematogaster sp. 2	1.32	0.95	1.39
Monomorium sp. 1	1.27	0.98	1.29
Small–large			
Pterostichinae sp. 2	2.34	0.76	3.06
Talistroides africana	1.67	1.18	1.42
Crematogaster sp. 2	1.47	0.85	1.73
Staphylinidae sp. 6	1.34	0.55	2.43
Tetramorium avium	1.23	0.72	1.71
Medium–large			
Pterostichinae sp. 2	1.81	0.71	2.55
Metaxinidium nanum	1.50	0.47	3.20
Tetramorium avium	1.22	0.85	1.44
Nemesiidae sp. 1	1.06	0.79	1.35
Staphylinidae sp. 13	1.04	0.79	1.32

two *Crematogaster* species and *Monomorium* sp. 1 were consistently the best discriminators, while for Araneae and Staphylinidae, the best discriminators were generally also the most abundant species. Using all species captured (including *T. africana*), five discriminating species were identified per paired patch size comparison. *T. avium* occurred in all three comparisons, while *Crematogaster* sp. 2, *T. africana* and Pterostichinae sp. 2 occurred in two patch-size comparisons.

Discussion

Invertebrate diversity in the naturally patchy forests

Little is known of the epigaeic invertebrate diversity in South African Afromontane forests. An electronic reference search (Agricola, Biological Abstracts, CAB and Life Sciences), showed that out of a total of 95 Afromontane studies, only 11 (12%) mentioned invertebrates, while the majority, 69 (76%), were related to flora. None of the 11 invertebrate-related studies focused on the epigaeic invertebrate fauna.

This lack of information, combined with the fact that the taxonomy of the invertebrate fauna in the region is poorly understood, make studying epigaeic invertebrates challenging. Studies are urgently needed in the Afromontane forest system, since this is one of the smallest, and most threatened ecosystems in the country. According to Geldenhuys and MacDevette (1989) 19161 ha of a total of 40141 ha of Afromontane forest are protected. Even though this is a relatively high percentage (almost 50%), the small number of larger forest patches left are separated by large zones of no forest, and in some places only small, fragmented and isolated forest patches are left (Geldenhuys and MacDevette, 1989). Furthermore, Teketay and Grandstrom (1995) found that most Afromontane tree species have relatively large seeds and poor long-distance dispersal, implying that natural regeneration of Afromontane forests after destruction is unlikely.

The small forest patches selected in this study reflect the size distribution of the forest fragments in the Afromontane region. Forest patches are situated in a disturbed, mainly agrocommercial landscape (Orthophoto survey, Surveyor General Office, Pietermaritzburg). *Talistroides africana*, an active litter decomposer (Friend and Richardson, 1986) occurred in abundance in these small patches. Consequently, this species can be an excellent indicator of environmental conditions. For example, only seven *T. africana* individuals were captured in the smallest forest patch here, compared to high abundances in the larger patches (see Appendix). Decomposers break down organic matter and engineer the epigaeic habitat (Stork and Eggleton, 1992), and a marked reduction in their numbers, as seen here, may cause a ripple effect in the community (Angelstam, 1992; Forman, 1995). *Talistroides africana* was also a good discriminating species, in terms of epigaeic invertebrate assemblage-structure, between small and medium, and small and large patches. More research, however, is needed to determine this species' usefulness as an indicator, since its low abundance in small patches may simply be because of an intrinsic feature of its population dynamics, and not a consequence of its sensitivity to environmental perturbations (Samways, 1994) or small forest patch-size.

Carabid species richness was very low in this study, which may be a consequence of several factors. The pitfall traps were small (diameter ca. 25 mm), with many large carabid species not being captured (Luff, 1975). We used the Majer (1978) trap since it was easy to install, ideal for sequential sampling, may be less susceptible to 'digging-in' effects than conventional traps (Greenslade, 1973; Digweed *et al.*, 1995), and captures a large number of small species, especially ants. Smaller traps are more efficient in capturing smaller species (Adis, 1979; Luff, 1975), which are usually the larger proportion of a community (May, 1981, 1989).

Carabid species richness may be depauperate in high-altitude Afromontane forests. This study was conducted on small species in forest patches situated at an altitude of above 1800 m a.s.l., and it is known that invertebrate species richness decreases with altitude in this part of South Africa (Samways, 1989). Moreover, the forest patches were small and discreet units with possibly little exchange of invertebrate individuals. Low carabid diversity in these patches might therefore be explained by local extinctions in individual small patches not being rescued by immigrations from other, larger, sparsely distributed forest patches (MacArthur and Wilson, 1967; Wu and Vankat, 1995). The carabid assemblage was dominated by a single species, Pterostichinae sp. 2, which made up 77% of the total carabid abundance. A decrease in diversity is often the result of a corresponding increase in the percentage dominance of a common species (Kempton, 1979; May, 1981). Moreover, this species was dominant only in the large forest patch and was a major contributor to the low diversity measure there. The smaller forests showed a much lower Pterostichinae sp. 2 abundance, and, combined with a more evenly distributed abundance among species, showed higher diversity values (Table 2; Fig. 3 – rarefaction).

Formicidae showed a similar species dominance pattern to that of Carabidae, with a single species, *Crema-*

togaster sp. 1, contributing to 68% of total ant abundance. Ants were, however, more species rich, with 19 species in total captured. Ants may find it easier to colonize isolated forest patches, a consequence of many ant species producing alate reproductive casts (Hölldobler and Wilson, 1990).

Both Araneae and Staphylinidae showed a more evenly-distributed abundance pattern than carabids or ants, i.e. there was no single dominant species. This was also reflected in the diversity indices, where spiders and staphylinids generally displayed higher diversity values than did carabids and ants. Spiders were the most species rich group, with 34 species captured. Van der Merwe *et al.* (1996) and Churchill (1997) argued that spiders operate as a dominant predator complex which can influence the structure of terrestrial invertebrate communities.

Lövei and Sunderland (1996) argued that carabids share the generalist, surface-active predator guild with some spiders and ants, and that significant competition for space and resources can take place between ants and carabids. Some competition is also quite likely to take place between other surface dwelling predacious groups (Thiele, 1977) in the same guild, such as staphylinids and spiders (Hawkins and MacMahon, 1989; Putman, 1994).

Habitat edges influence species distribution, genetic structure and predation (Yahner, 1988; Risser, 1995). Species richness of Carabidae, Staphylinidae and Formicidae did not change significantly from forest interior to edge, but that of Araneae did (Table 1). In contrast, abundances of Amphipoda, Staphylinidae as well as Araneae changed from forest interior to edge, whereas that of Carabidae and Formicidae did not. These results suggest that edge effects play a major role in the diversity patterns observed among some of the taxa selected.

Multi-taxa, or 'shopping basket' approach to invertebrate conservation

Invertebrates, being dominant in species richness and abundance, are linked to critical ecological processes and ecosystem functioning (McGeoch, 1998). They also provide quantitative data from small spatial scales (Churchill, 1997). Due to their hyperdiverse nature (Colwell and Coddington, 1994), however, it is impossible to accurately sample all invertebrate taxa (Samways, 1994), hence many conservation studies have focused on a single, indicator, invertebrate taxon (New, 1994). As well as being diverse and abundant, taxonomically well-known, readily-sampled, functionally-significant, and showing predictable responses to disturbance or environmental change (Brown, 1991; Churchill, 1997), the diversity of biodiversity indicator taxa ideally should also positively correlate with diversities of other taxa (Hammond, 1994; Oliver and Beattie, 1996; McGeoch, 1998; Niemelä and Baur, 1998).

In this study, the only significant positive correlation in terms of species richness was between Carabidae and Staphylinidae, while Formicidae species richness correlated negatively with that of Araneae, Carabidae and Staphylinidae. These results demonstrate that trends in one taxon may not indicate similar trends in others, and support the multi-taxa, or 'shopping basket' approach to monitoring (Hammond, 1990; Stork and Brendell, 1990; di Castri *et al.*, 1992; Stork, 1994, 1995). This concords with Lawton *et al.* (1998), Niemelä and Baur (1998), and Oliver *et al.* (1998) who found that no one group served as a good indicator taxon for others, since phylogenetically distant groups have very different ecological requirements. Lawton *et al.* (1998) did, however, find a significant positive correlation between canopy ants and canopy beetles, two groups occupying the same habitat. In contrast, we show here that for epigaeic ants, two beetle families and spiders, there was not a good correlation.

Overall, all taxa showed significant differences in assemblage-structure among forest patches, suggesting community change, or turnover, both in terms of composition and structure (Clarke, 1993; Oliver and Beattie, 1996). This is shown by the high variability in species composition among the patches and taxa, as was illustrated by the complementarity analysis. This assessment of turnover is important for determining complementarity, or representativeness, and is essential for setting conservation priorities (Pressey *et al.*, 1994; Oliver and Beattie, 1996; Reid, 1998). Ants, for example, consistently shared few species between categories, while staphylinids shared many (see also Appendix). Conservation decisions based on ant data alone would differ considerably from those based on staphylinids. Ant data suggest that all patches should be considered for conservation (high complementarity), while staphylinid data suggest that the categories selected were quite similar in species composition (low complementarity), and that perhaps only the larger patches warrant conservation consideration. These results add the Afromontane forest complex to the already growing amount of evidence for multi-taxa studies in biodiversity conservation (various forest types in Australia – Oliver and Beattie (1996), tropical forests in Cameroon – Lawton *et al.* (1998), and calcareous grassland in Switzerland – Niemelä and Baur (1998)).

In conclusion, this study supports the multi-taxa approach to conservation studies and habitat evaluation. We selected an important component of terrestrial diversity (epigaeic invertebrates) and Koen and Crowe (1987) showed that ground invertebrates were better habitat predictors than litter or aerial invertebrates. Selecting the 'correct' suite of organisms, however, still poses a problem. We focused our research on four relatively well-known epigaeic invertebrate taxa, but we cannot state that these groups positively reflect the diversity patterns of others: they do not even positively reflect the diversity pattern of one another. Reid (1998) argued that, at fine scales of geographic resolution, taxonomic groups are likely to contain species that share narrow habitat requirements, thus areas of high diversity for those samples are less likely to correspond across taxonomic groups. The next research step would be to correlate the diversities of other organisms from the same stratum and from other forest strata. This has been done in other systems (Lawton *et al.*, 1998) and the general conclusion is that different organisms showed little correlation in terms of species richness. The question remains: is the indicator concept appropriate when we are seeking to assess biodiversity, or *are* all species equal . . . ?

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Appendix. Amphipoda, Araneae, Carabidae, Staphylinidae and Formicidae species captured and their respective abundances

	Small patches		Medium patches			Large patch				
	P1 set 1	P2 set 1	P3 set 1	P4 set 1	P4 set 2	P5 set 1	P5 set 2	P5 set 3	P5 set 4	P5 set 5
Amphipoda										
Talistroides africana (Griff.)	7	229	292	88	240	603	481	428	205	102
Araneae										
Amaurobiidae sp. 1	3	1	6	1	1	1	2	0	0	2
Amaurobiidae sp. 2	0	0	0	0	0	0	2	0	0	0
Clubionidae sp. 1	0	0	0	0	0	1	0	0	0	0
Gnaphosidae sp. 1	1	0	3	0	0	0	1	1	0	0
Gnaphosidae sp. 2	0	0	0	0	0	0	0	1	0	0
Hahniidae sp. 1	1	4	6	2	2	6	1	1	5	6
Linyphidae sp. 1	0	4	0	0	0	3	6	6	2	2
Miturgidae sp. 1	0	0	0	0	0	0	0	0	1	0
Miturgidae sp. 2	0	3	0	1	1	3	2	0	1	1

Appendix. *continued*

	Small patches		Medium patches			Large patch				
	P1 set 1	P2 set 1	P3 set 1	P4 set 1	P4 set 2	P5 set 1	P5 set 2	P5 set 3	P5 set 4	P5 set 5
Nemesiidae sp. 1	4	0	0	0	0	9	3	0	8	12
Nemesiidae sp. 2	1	1	0	1	1	4	0	3	2	0
Nemesiidae sp. 3	1	0	0	0	0	0	0	0	0	0
Oonopidae sp. 1	1	3	5	0	2	1	8	4	1	4
Salticidae sp. 1	0	0	0	0	1	1	0	1	0	0
Salticidae sp. 2	3	2	0	2	10	9	5	14	11	7
Salticidae sp. 3	1	0	0	0	0	0	0	0	0	0
Scytodidae sp. 1	2	2	8	2	0	0	0	1	1	2
Tetragnathidae sp. 1	0	1	1	0	2	3	3	3	1	5
Theriidae sp. 1	0	0	0	1	0	0	0	0	0	0
Thomisidae sp. 1	0	0	1	0	0	0	0	0	0	0
Zodariidae sp. 1	0	0	0	0	0	0	0	1	0	0
Zodariidae sp. 2	0	3	2	0	0	0	1	1	1	0
Zodariidae sp. 3	0	0	5	0	0	0	1	1	0	1
Zodariidae sp. 4	0	2	0	0	0	2	0	0	2	1
Zodariidae sp. 5	3	4	11	7	6	12	4	11	2	12
Zodariidae sp. 6	0	0	0	0	0	2	5	0	0	0
juvenile sp. 1	0	1	0	0	1	4	0	1	0	2
juvenile sp. 2	0	0	0	0	0	0	1	0	2	0
Araneae sp. 1	11	9	11	14	5	15	20	19	7	12
Araneae sp. 2	5	1	4	30	45	19	7	3	6	16
Araneae sp. 3	0	1	0	0	1	0	0	3	2	0
Araneae sp. 4	32	31	9	10	7	17	27	20	11	17
Araneae sp. 5	0	4	2	2	1	3	6	2	0	0
Araneae sp. 6	0	0	0	0	0	0	0	0	1	0
Carabidae										
Harpalinae sp. 1	0	1	0	0	3	2	0	2	1	0
Harpalinae sp. 3	3	2	3	0	8	22	12	4	2	10
Pterostichinae sp. 2	2	2	3	2	9	89	117	88	53	149
Pterostichinae sp. 4	2	0	0	0	0	0	0	0	0	0
Pterostichinae sp. 3	3	1	5	0	3	0	0	0	0	2
Haplotrachelus sp. 1	0	0	0	0	0	1	1	1	1	0
Metaxinidium nanum Basil.	0	5	0	0	0	15	14	2	7	9
Tyronia sp. 1	0	0	0	0	0	1	0	0	0	0
Xenitenus sp. 1	0	1	0	0	2	0	0	0	0	0
Staphylinidae										
Staphylinidae sp. 1	0	1	3	5	0	5	2	7	7	13
Staphylinidae sp. 2	1	0	0	0	0	0	0	0	0	0
Staphylinidae sp. 3	0	0	0	0	0	0	1	0	0	0
Staphylinidae sp. 4	0	1	0	0	0	2	4	0	2	2
Staphylinidae sp. 5	3	1	0	0	11	0	4	1	6	1
Staphylinidae sp. 6	0	1	1	2	2	6	5	5	10	6
Staphylinidae sp. 7	8	7	7	6	14	38	28	12	17	30
Staphylinidae sp. 8	10	7	21	12	27	30	27	36	35	20
Staphylinidae sp. 9	3	0	1	1	5	2	0	0	1	2

Appendix. *continued*

	Small patches		Medium patches			Large patch				
	P1 set 1	P2 set 1	P3 set 1	P4 set 1	P4 set 2	P5 set 1	P5 set 2	P5 set 3	P5 set 4	P5 set 5
Staphylinidae sp. 10	41	12	72	76	122	131	101	104	119	125
Staphylinidae sp. 11	27	19	63	97	30	87	78	47	66	51
Staphylinidae sp. 12	42	39	110	19	50	153	230	78	69	20
Staphylinidae sp. 13	0	1	0	0	0	15	7	3	5	2
Staphylinidae sp. 14	1	17	34	0	11	13	12	10	8	8
Staphylinidae sp. 15	0	0	3	0	0	0	1	0	0	0
Staphylinidae sp. 16	7	6	1	3	4	10	4	4	4	1
Formicidae										
Streblognathus aethiopicus Smith, 1958	0	0	1	0	0	0	0	0	0	0
Pachycondyla peringueyi Emery, 1899	0	1	1	13	0	0	0	0	0	0
Pachycondyla wroughtoni Forel, 1901	4	0	0	1	11	0	0	0	0	0
Hypoponera transvaalensis Arnold	0	0	0	0	3	0	0	0	0	0
Leptogenys intermedia Emery, 1902	0	1	1	1	6	0	0	0	0	0
Dorylus sp.	0	0	0	10	33	0	0	0	0	0
Camponotus niveosetosus Mayr, 1862	0	0	0	1	0	1	0	0	0	0
Crematogaster sp. 1	114	272	59	133	119	93	108	103	28	78
Crematogaster sp. 2	2	28	0	3	3	0	0	0	0	2
Meranoplus peringueyi Emery, 1886	4	0	3	0	0	0	0	0	0	0
Solenopsis punctaticeps Mayr, 1865	0	1	0	0	0	0	0	0	0	0
Tetramorium avium Bolton, 1980	38	0	2	130	32	10	1	11	3	15
Tetramorium setigerum Mayr, 1901	0	0	0	1	0	0	0	0	0	0
Tetramorium sp. – *squaminode*-group	0	0	0	1	0	0	0	0	0	0
Rhoptromyrmex n. sp.	0	0	0	8	0	0	0	0	0	0
Calyptomyrmex clavisetus Santschi, 1914	0	0	6	0	0	17	0	0	0	0
Pheidole sp. 1	16	0	0	2	1	0	0	0	1	0
Monomorium sp. 1 – *monomorium*-group	28	5	1	10	1	17	0	0	2	26
Monomorium sp. 2 – *monomorium*-group	0	0	0	0	0	0	0	2	0	0
Totals										
Individuals										
Amphipoda	2675									
Araneae	865									
Carabidae	665									
Staphylinidae	3001									
Formicidae	1629									
Species										
Araneae	34									
Carabidae	9									
Staphylinidae	16									
Formicidae	19									

Abbreviations: P1 = patch 1, P2 = patch 2 .... Transect sets are explained in the text.

II

(Manuscript under review)

Invertebrate diversity at forest-grassland ecotones in an Afromontane forest landscape in South Africa

D.J. Kotze and M.J. Samways

Abstract

The Afromontane region of South Africa is characterised by numerous small, natural forest patches in a grassland matrix. The edges, or ecotones between forest and grassland are usually sharp (a few metres) and are maintained both naturally and, more recently, anthropogenically. We investigated distribution patterns of epigaeic invertebrates and abiotic environmental variables across these forest-grassland ecotones. The biological edge effect hypothesis at ecotones was not supported by our data as neither carabids nor ants showed an increase in abundance or species richness at these natural ecotones. Five of the 37 sampled species, however, did increase in abundance at the ecotone. In particular, the amphipod *Talistroides africana* was significantly more numerous at edges than in either forest or grassland interiors. Overall, carabids were more abundant and species rich in the forests, while ants showed a preference for the grasslands. We propose that edge effects are not a characteristic of natural habitat boundaries, but mainly of anthropogenically-created ones. Furthermore, we argue that a conservation strategy for the natural Afromontane forest patches must also incorporate the surrounding *Themeda triandra* dominated grasslands. The grassland habitat is often perceived as less valuable than forests and, as a consequence, is subject to many anthropogenic disturbances such as cattle grazing and afforestation. Protecting grasslands around forest patches not only conserves the rich ant diversity but also conserves the biota at the forest-grassland ecotone.

Introduction

In heavily-fragmented landscapes, habitat edges, or ecotones, become a major, even dominant feature (Laurance, 1997). An ecotone is a zone of transition between adjacent ecological systems, having characteristics uniquely defined by space and time scales and by the strength of the interactions between the adjacent ecological systems (Holland and Risser, 1991). Ecotones may be abrupt or gradual, with disturbance tending to increase the abruptness of the ecotone (Forman and Godron, 1981). Edge effects, manifested as elevated species richness (Odum, 1971; Rapoport *et al.*, 1986; Murcia, 1995; Risser, 1995), as a change in species interactions (Wilcove *et al.*, 1986; Andrén and Angelstam, 1988) or abiotic factors (see Murcia, 1995), are often associated with ecotones.

Despite the wealth of information available on edge effects that result from anthropogenic fragmentation (Hansen *et al.*, 1988; Andrén, 1995; Kapos *et al.*, 1997; Laurance, 1997), little is known on biological and abiotic patterns and processes across natural habitat boundaries, especially sharp ones. Didham (1997) pointed out that an increase in insect abundance and diversity at forest edges is almost certainly a result of invasion of generalist species from disturbed habitats outside the forest fragment. The question is then, whether edge effects are a characteristic of natural habitat boundaries, or whether they are an artefact of anthropogenically-created landscapes. The role of edge effects and ecotones in biotic communities is, however, poorly understood, especially in tropical and subtropical countries (Samways, 1994).

Natural forest patches in the Afromontane region have been changing in size and connectivity for, perhaps, millions of years (Lawes, 1990). Over the last 300 years, however, human disturbances have greatly reduced forest extent (Geldenhuys and Knight, 1989). But unlike complete destruction of forests through logging and clear-cutting, the small Afromontane forests have mainly experienced disturbances such as selective log removal within the patches, and fire damage at the margins (Everard, 1986). Indeed, fire is a main anthropogenic disturbance in the *Themeda triandra* Forssk. dominated Afromontane grasslands today, but since fire is also a regular natural event in this region, deliberate fires simulate natural conditions. In fact, it appears that *T. triandra* dominated grasslands require fire, at least once every two to three years, to maintain native plant diversity and health and vigour of this grass itself (Morgan and Lunt, 1999). The fire simulation is not exact, however, as fires are now more frequent and occur more often in the winter months than would be the case naturally (Tainton, 1981; Everard, 1986). Fire is responsible for the extreme sharp (a few metres) transition between forest and grassland.

The aim of this study is to focus on near-natural, sharp Afromontane forest-grassland ecotones to determine whether there is an edge effect of elevated invertebrate abundance and species richness, and invertebrate compositional changes across these ecotones. Furthermore, we selected a number of environmental variables across these ecotones to investigate abiotic change from forest to grassland.

The invertebrate taxa selected are ground beetles (Carabidae), and ants (Formicidae), both of which have been used extensively in ecological assessments (e.g.

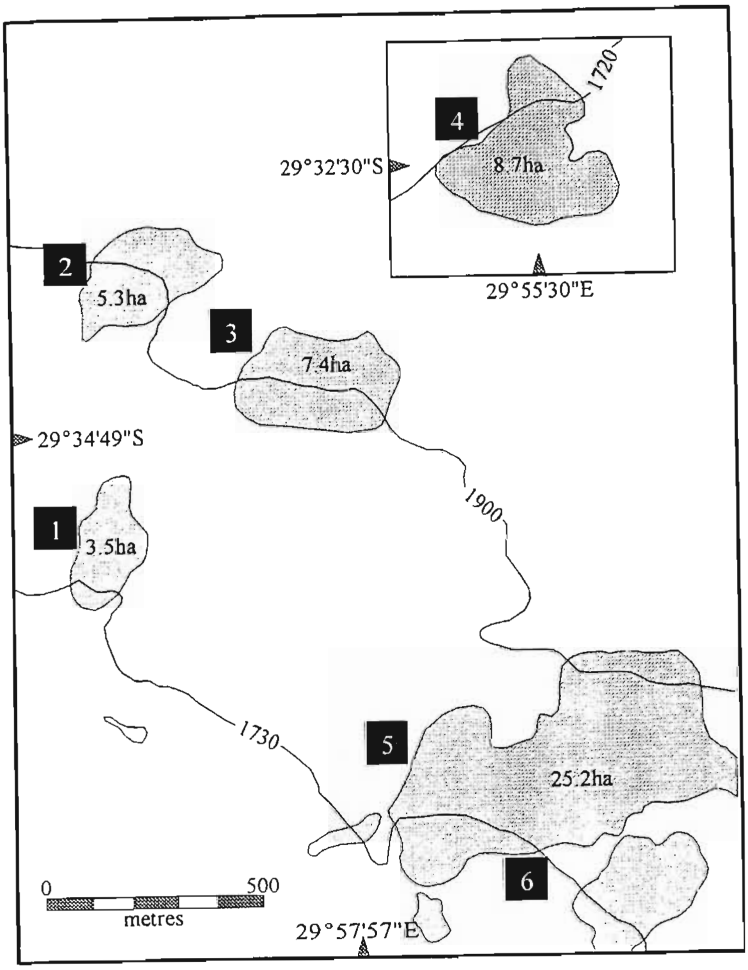

Fig. 1. Study sites selected in the KwaZulu-Natal midlands, South Africa. Numbers one to six are the locations of the transect-sets across the Afromontane forest-grassland ecotone. Shaded areas represent forest patches, while white areas are the grasslands.

Hill, 1995; Giller, 1996; Niemelä, 1996; Andersen, 1997), and the terrestrial amphipod *Talistroides africana* Griff. which is an abundant component of the Afromontane forest litter layer (chapter I).

Study area, materials and methods

Study area and site selection

Six forest-grassland sites (3.5 - 25.2 ha), within an Afromontane forest patch archipelago, were selected in the Impendle district, KwaZulu-Natal, South Africa, on the farm Nhlosane (29°35'S 29°58'E) (Fig. 1; see also chapter I). Sites were selected on the basis of similarity in edge vegetation structure. The forest interiors were dominated by *Podocarpus* spp., and the edges by the fire-resistant tree species *Leucosidea sericea* Eckl & Zeyh. (Acocks, 1988). All sites had sharp edges with the vegetation change from forest to grassland taking place within a few metres. Selection of sites also considered similarity in grassland matrices, which were dominated by redgrass, *Themeda triandra* Forssk. All sites were within a 5-km radius of one another, at a comparable elevation (between 1720 and 1900 m a.s.l.) and latitude. All were on the cooler south-facing slopes, which is the natural position of this type of forest.

Pitfall trapping layout

Invertebrates were captured using pitfall traps (mouth diameter = 25 mm, trap depth = 150 mm) (Majer, 1978). Trap transects were oriented perpendicular to the forest-grassland boundary, starting with a trap at the boundary, then placing a trap 1, 2, 4, 8, 16, 32 and 64 m into the forest and grassland respectively, giving a line transect of 15 traps, 128 m in length. Line transects were replicated three times, with transects 5 m apart, resulting in a transect-set of 45 traps. Forest patches that were not large enough to have a trap 64 m into the forest had a trap placed as close to the centre of the forest as possible. Sites one, two and three had one transect-set each, site four had two parallel transect-sets (a 100 m apart), and sites five and six had five parallel transect-sets each (100 m apart). The 100 m distance between parallel transect-sets was for independent sampling (Digweed *et al.*, 1995). More than a single transect-set at sites one, two and three, and two transect-sets at site four, could not be placed because of small forest-patch sizes (see also chapter I).

Trapping at all sites was early October 1993 to the end of December 1993. Trapping was continuous with two-week intervals. Trapped specimens were removed and traps refilled with a 20 mm ethylene-glycol: alcohol mixture (3:1). Amphipods, carabids and ants captured were identified to species level wherever possible.

Environmental variables selected

Variables were chosen on the basis of their possible significance in contributing to distribution patterns of amphipods, carabids and ants across the ecotones. Variables were measured, and adequately replicated, at each distance sampled across the gradient, per transect-set, and included: 1) temperature 10 mm above ground level; 2) temperature 10 mm below ground level; 3) relative humidity 10 mm above ground level; 4) soil pH; 5) percentage soil moisture; 6) percentage organic carbon; 7) soil compaction (measured in MPa); 8) depth of leaf litter (measured in mm); 9) percentage tree shade; 10) percentage ground cover; and 11) ground cover height (measured in mm). Temperature and relative humidity were measured during sunny days, once a week for the duration of the study period, using a hand held thermo-hygrometer (Model: HYGRO- THERMOMETER, Thies Clima, Germany). Soil pH, soil moisture and organic carbon were determined at the Soil Science Department of the University of Natal, by analysing field soil core samples (300 mm deep core samples). Soil compaction was measured using a simple hand held penetrometer and digitising equipment. Variables 9 to 11 were measured using 1 x 1 m quadrats at each pitfall trap.

Data analyses

Individual traps yielded low catch, possibly a consequence of both small trap mouth diameter and low invertebrate diversity at high altitudes (Samways, 1989). Therefore, the sum of individuals and species captured at each distance sampled, per transect-set of 45 traps was used in the analysis. This resulted in 15 values per distance treatment, for all sites combined, i.e. 15 values (for carabid species richness for example) at 64 m inside forests, 15 values at 32 m inside forests, and so on.

Species accumulation curves were constructed for both carabids and ants. Sampling order (i.e. trap order) was randomised 100 times to eliminate sampling error and heterogeneity among units sampled (Colwell and Coddington, 1994) and the mean and standard deviation of S(*n*) (number of species discovered) computed for each value of *n* between 1 and 225.

A two-level nested ANOVA was used to test for differences in carabid and ant abundance and species richness with patch size and, primarily, distance across the ecotone. Data used in the ANOVA were transformed to approximate normality to comply with parametric test assumptions (see Table 1) (Clarke and Warwick, 1994; Sokal and Rohlf, 1995). The Scheffé unplanned comparisons test was used to determine significance of differences among means, resulting from the ANOVAs (Sokal and Rolf, 1995).

Carabid and ant α-diversity were determined using Simpson's diversity index at each distance sampled across the ecotone, while turnover across the ecotone was determined using cluster analysis (group-average linking algorithm with Bray-Curtis similarity metric). Cluster analysis aims to find natural groupings of samples such that samples within a group are more similar to each other than samples in different groups (Clarke and Warwick, 1994). We also investigated population number changes of the most abundant species across these ecotones, using a simple forest interior: edge: grassland interior ratio (F:E:G) (F = traps from 64 to 4 m inside forests, E = traps from 2 m inside forests to 2 m inside grasslands, and G = traps from 4 to 64 m inside grasslands). The greater the ratio of density at the edge to density in the habitat interior, the greater the edge effect (Kroodsma, 1984).

To find potential predictors of mean amphipod abundance, and mean carabid and ant abundance, species richness and diversity, all variables selected, including distance across the ecotone, were used in stepwise multiple regression analysis.

Results

Dominant species

One amphipod species, *Talistroides africana,* (4 854 individuals), 13 carabid species (1 517 individuals) and 23 ant species (4 827 individuals) were captured (Appendix). The dominant carabid was Pterostichinae sp. 2 (73.7%), with nine times more individuals captured than the second most abundant carabid species, Harpalinae sp. 3 (8.2%). The five most abundant carabid species contributed 96% of total carabid abundance. The most abundant ant species captured was *Crematogaster* sp. 1 (40.4%), almost three times more abundant than the second most abundant ant species, *Tetramorium avium* (14,5%). The 12 most abundant ant species contributed 96% of total ant abundance.

Both carabid and ant accumulation curves reached their respective asymptotes, indicating that most species in these assemblages were accounted for (Fig. 2).

Spatial variation across the ecotones

Significantly different mean numbers of carabid individuals and species were captured between the six sites selected (Table 1). Carabid abundance was high at 64 m inside forests, and decreased significantly to a low at 64 m into grasslands (Table 1; Fig. 3A). Carabid species richness also decreased from forest to grassland, but not significantly (Table

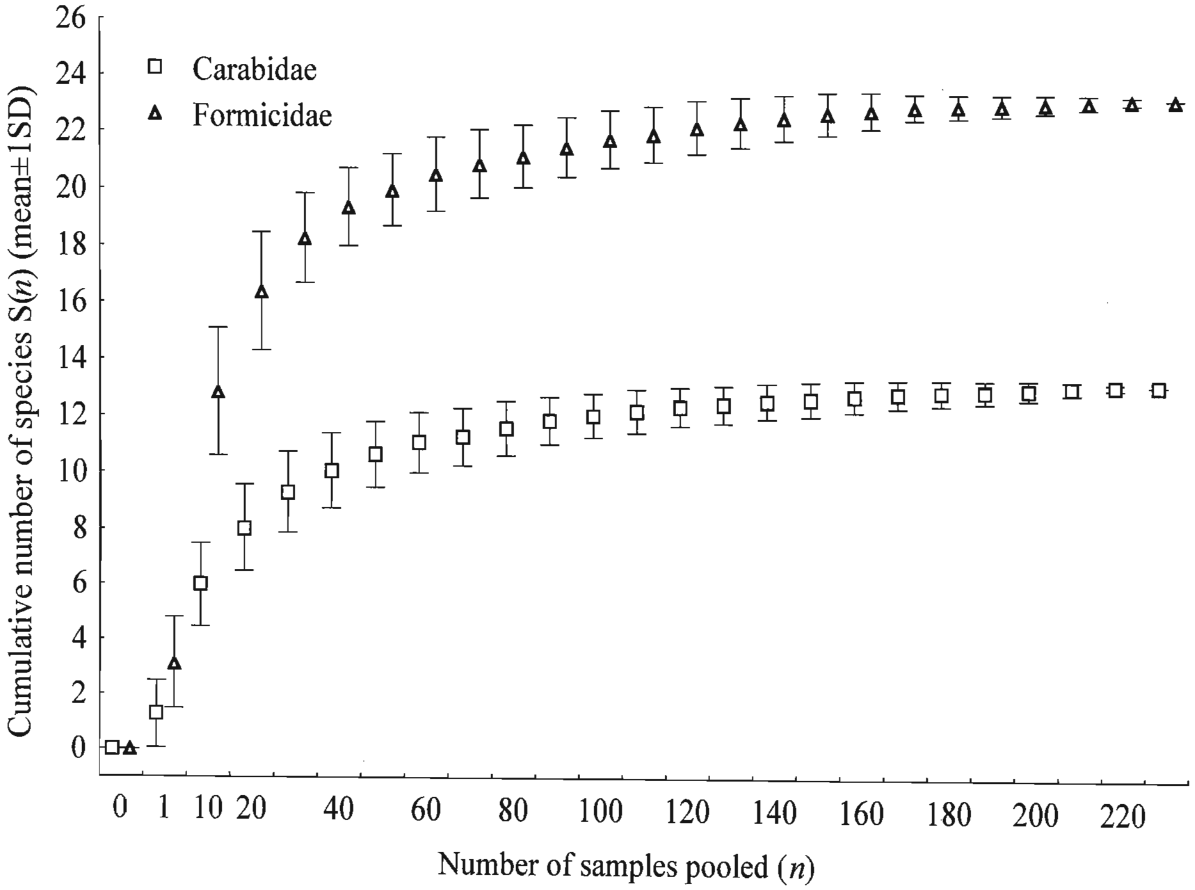

Fig. 2. Carabid and ant species accumulation curves. Both taxa reached their respective asymptotes after 225 traps pooled. Points represent mean values, while bars are one standard deviation (see text for details).

1; Fig. 3B). Interestingly, 12 carabid species were captured in the grasslands whereas only 10 occurred in the forests. Also, three species occurred only in the grasslands while only one carabid occurred exclusively in the forests (Appendix). Mean ant abundance and species richness differed significantly between the six sites selected (Table 1). Although ant abundance did not change significantly across the ecotone (Table 1; Fig. 4A), species richness did increase significantly from 64 m inside forests to 64 m into grasslands (Table 1; Fig. 4B).

Carabid diversity (reciprocal of Simpson's index; 1/D) varied considerably across the ecotone, with no correlation between species richness and diversity, while ant diversity followed the ant species richness pattern (Pearson correlation: $r = 0.82$, $df = 13$, $p < 0.001$) (Table 2).

Changes in carabid and ant assemblage-structure, across the ecotones, were illustrated using cluster analysis (Fig. 5). For carabids, two distinct clusters formed at 60% similarity; a forest-edge cluster, including traps placed up to 4 m into grasslands, and a grassland cluster; with traps placed from 8 to 64 m into grasslands (Fig. 5A). Ant assemblage separated into three distinct clusters at 70% similarity; a forest cluster (8 to 64 m inside forests), a cluster at the ecotone (from 4 m inside forests to 4 m inside grasslands), and a grassland cluster (8 to 64 m inside grasslands) (Fig. 5B).

Significantly more *Talistroides africana* ($F = 5.26$, $p < 0.001$) individuals were captured at the ecotone than in habitat interiors. The ant *Crematogaster* sp. 1 ($F = 9.83$, $p < 0.001$) was significantly more abundant in forests and at ecotones than in grassland interiors, while the carabids Pterostichinae sp. 2 ($F = 8.75$, $p < 0.001$) and Harpalinae sp. 3 ($F = 3.21$, $p < 0.001$) were both significantly more abundant in forests than at ecotones or in grasslands. Although not significant, the ant *Meranoplus peringueyi* ($F = 1.64$, $p = 0.07$) was mainly absent from forests and abundant in grasslands (Fig 6). In all, five

Table 1. One-way analysis of variance showing differences between mean number of carabid and ant individuals and species captured across the forest-grassland ecotones.

Invertebrate group	Source of variation	df	MS	F	p
Carabidae					
Individuals	Among sites	5	2.852	18.855	< 0.001
(√√-root)	Among distances across the ecotones	84	0.273	1.804	= 0.001
	error	135	0.151		
Species	Among sites	5	9.696	9.173	< 0.001
(none)	Among distances across the ecotones	84	1.287	1.217	0.154ns
	error	135	1.057		
Formicidae					
Individuals	Among sites	5	1.594	11.679	< 0.001
(log)	Among distances across the ecotones	84	0.138	1.013	0.467ns
	error	135	0.137		
Species	Among sites	5	2.645	13.540	< 0.001
(√-root)	Among distances across the ecotones	84	0.415	2.124	< 0.001
	error	135	0.195		

Transformation technique used are indicated in parentheses. df = degrees of freedom, MS = mean square, ns = not significant.

species showed an affinity for edge habitat (*Talistroides africana, Pachycondyla wroughtoni, Calyptomyrmex clavisetus, Dorylus* sp., and *Tetramorium avium*), four for forest habitat (Pterostichinae sp. 2, Harpalinae sp. 3, *Metaxinidium nanum* and *Crematogaster* sp. 1) and five for grassland habitat (*Haplotrachelus* sp. 1, *Pachycondyla peringueyi, Meranoplus peringueyi, Pheidole* sp. 1 and *Tetramorium* sp. squaminode-group),

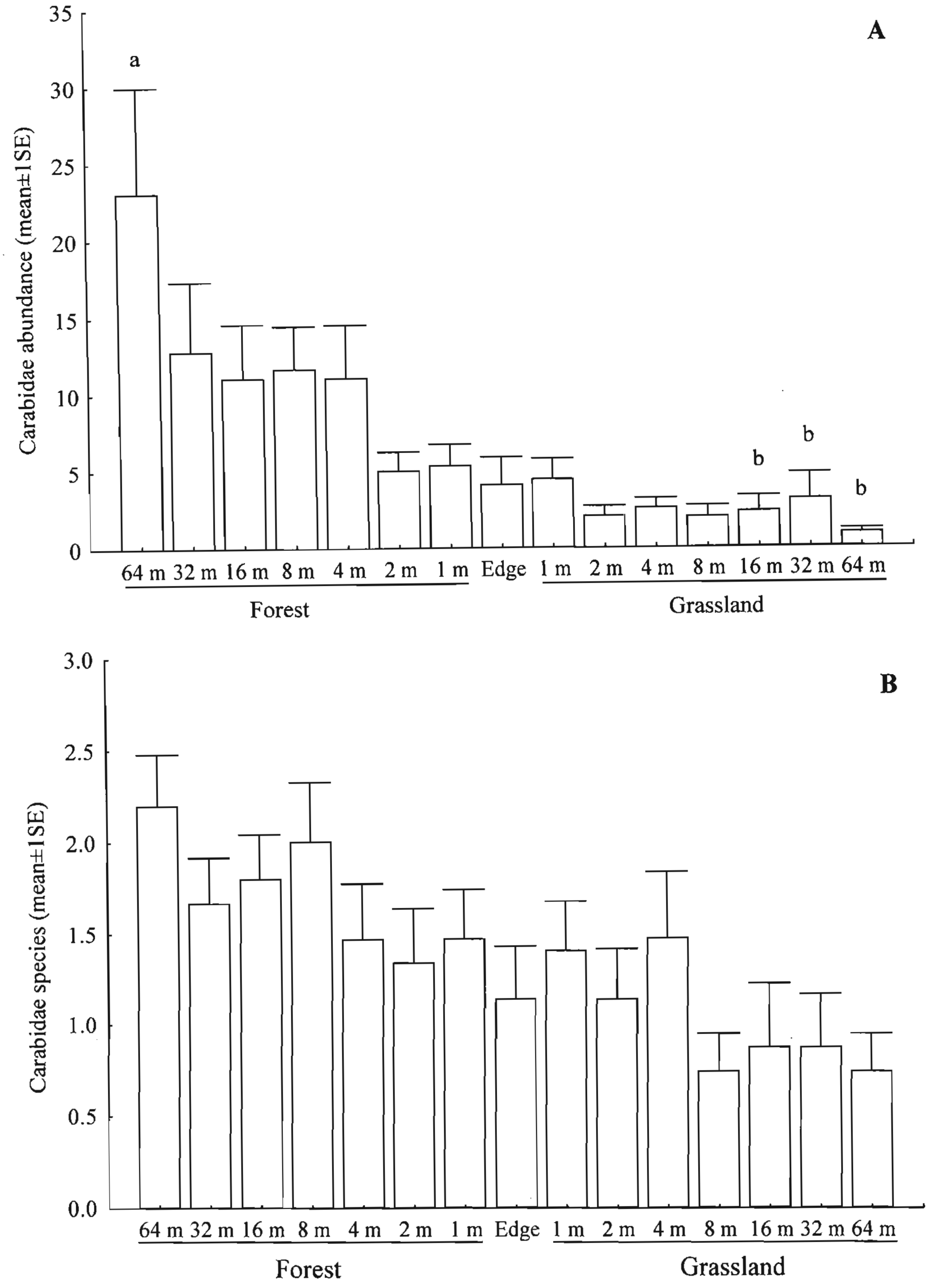

Fig. 3. A - Mean (±1SE) carabid abundance across the forest-grassland ecotone, **B** - mean (±1SE) carabid species richness across the ecotone. Different letters above bars represent significantly different means (at the 5% level).

some statistically, see above, others not.

Alternatively, the forest interior: edge: grassland interior ratio (F:E:G), described above, can be used to illustrate a species' affinity to forest, edge or grassland. For example, *Talistroides africana* had a F:E:G ratio of 21:64:15 while the ant *Calyptomyrmex clavisetus*, a ratio of 9:79:12, and the ant

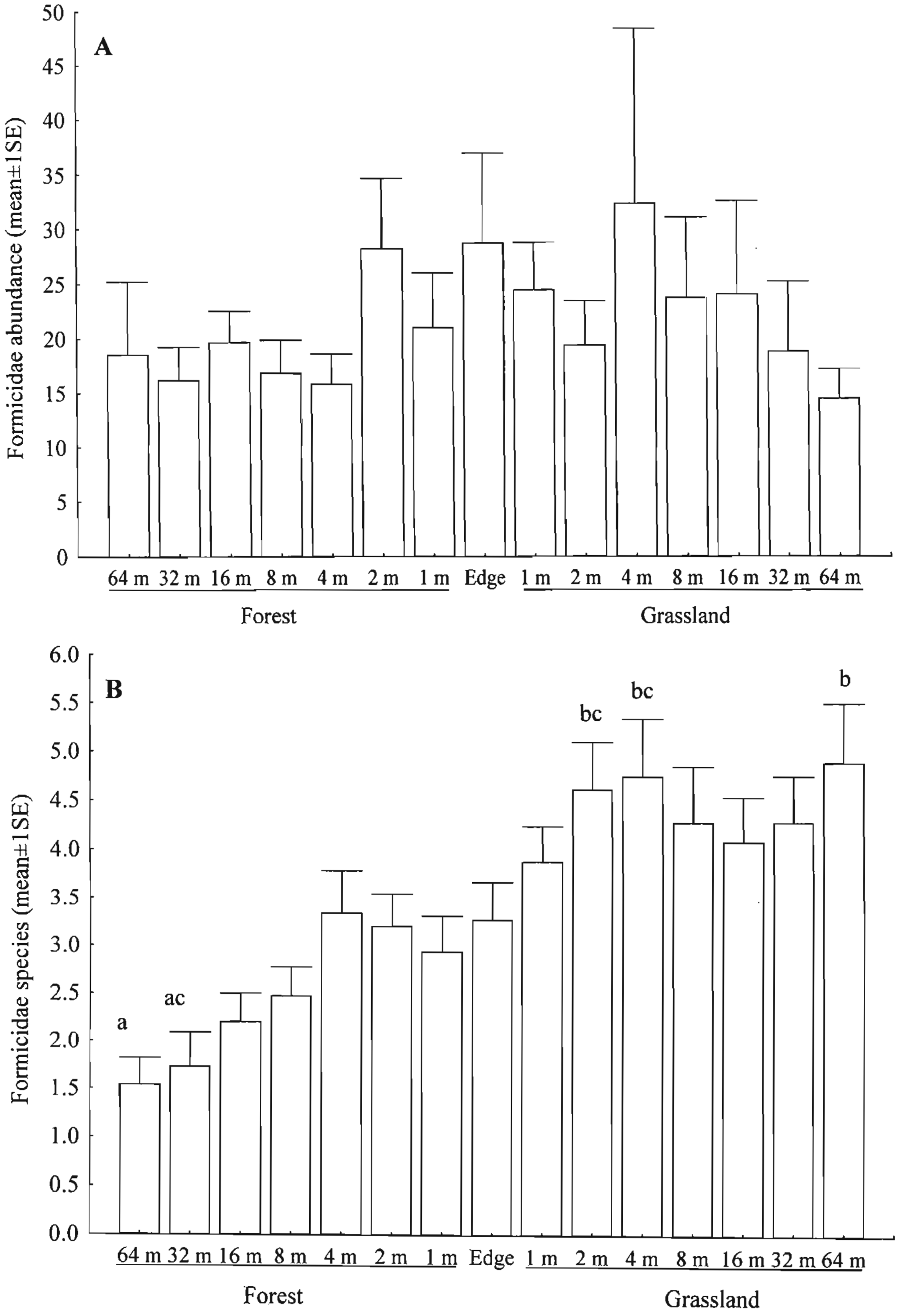

Fig. 4. **A** - Mean (±1SE) ant abundance across the forest-grassland ecotone, **B** - mean (±1SE) ant species richness across the ecotone. Different letters above bars represent significantly different means (at the 5% level).

Table 2. Carabid and ant diversity (measured as Simpson's diversity index (1/D)) across the forest-grassland ecotone. Mean ±1SD values are given.

Invertebrate	Forest*								Grassland*						
group	64	32	16	8	4	2	1	E	1	2	4	8	16	32	64
Carabidae															
Mean	1.92	1.44	1.78	2.46	1.88	1.84	2.14	2.76	2.54	1.99	2.35	1.46	1.37	1.81	3.00
SD	1.52	0.64	1.42	2.61	0.86	1.63	1.67	2.50	2.08	0.74	1.11	0.87	0.55	0.44	0.00
Formicidae															
Mean	1.37	1.43	1.87	2.15	2.59	2.73	2.73	2.23	2.46	3.39	3.29	3.53	4.72	5.26	5.13
SD	0.66	0.65	0.89	1.20	1.37	2.25	1.25	1.19	0.90	1.49	1.47	1.74	2.49	5.26	2.63

* values below forest and grassland headings represent distances (in metres) into that habitat, i.e. the first 64 represents 64 m into forest, while the second 64 represents 64 m into grassland. E = edge.

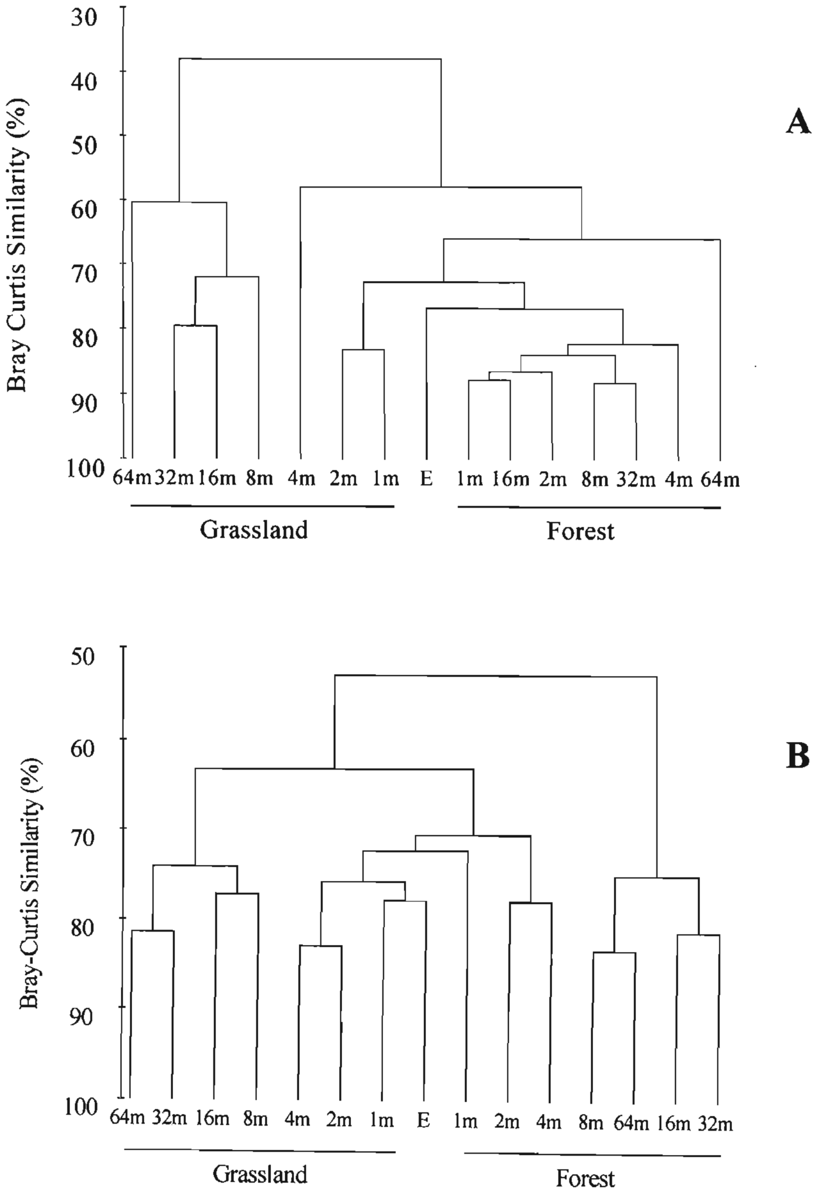

Fig. 5. Cluster analysis, using Bray-Curtis similarity matrices, to construct dendograms for both carabid (**A**) and ant (**B**) assemblages across the ecotone. At 60% similarity the carabid assemblage divided into two distinct clusters; a forest-edge cluster (from 64 m inside forest to 4 m inside grassland), and a grassland cluster (from 8 to 64 m into grassland). Ant assemblage divided into three distinct clusters at 70% similarity; a forest cluster (64 to 8 m inside forest), a transitional zone cluster (4 m inside forest to 4 m inside grassland), and a grassland cluster (from 8 to 64 m inside grassland).

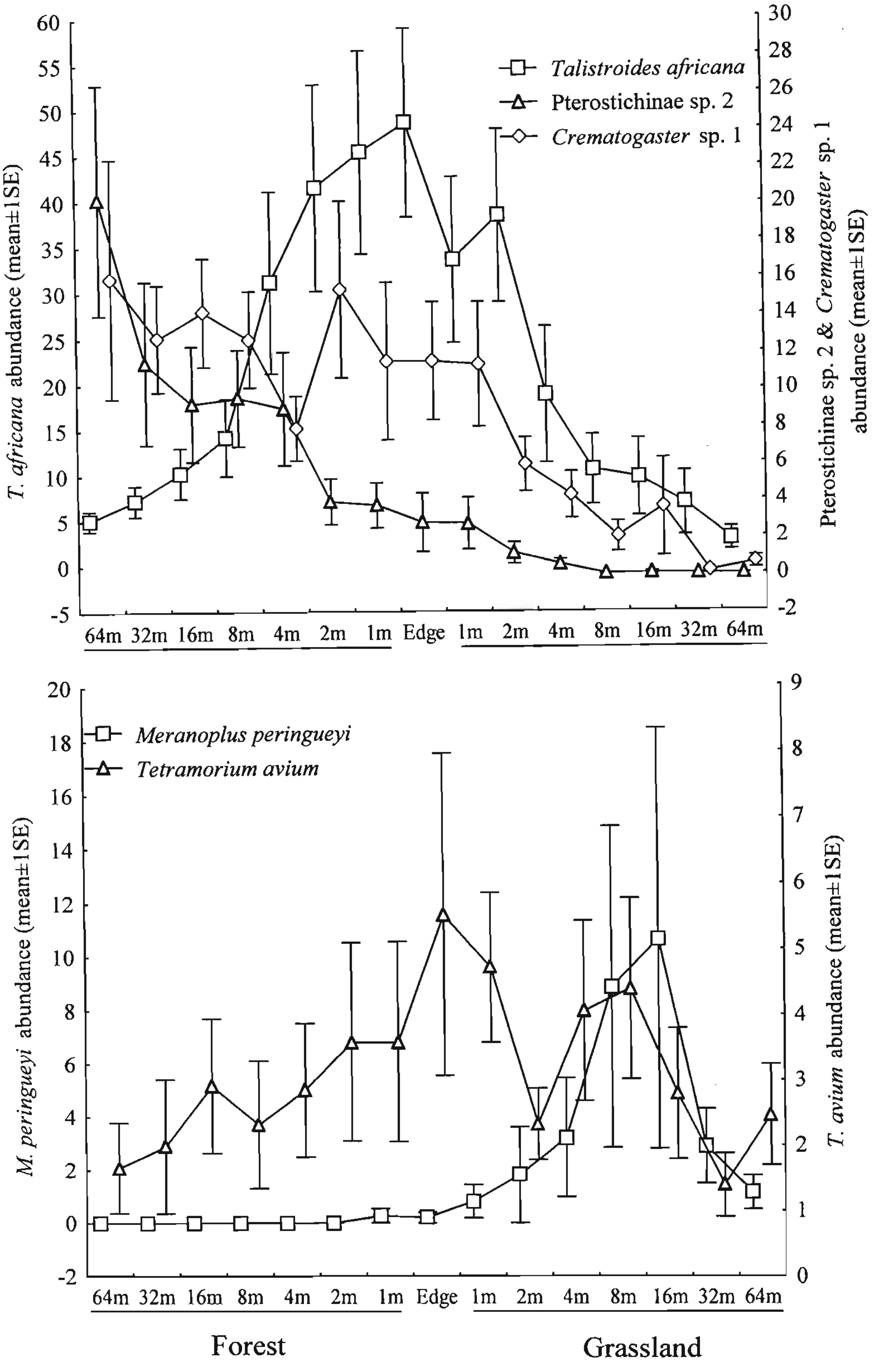

Fig. 6. Distribution patterns of the five most abundant species captured across the ecotones. *Talistroides africana* and *Tetramorium avium* showed an increase in abundance at the ecotone, while Pterostichinae sp. 2 and *Crematogaster* sp. 1 were more abundant in forests than grasslands. *Meranoplus peringueyi* was absent from forests, but abundant in grasslands. Note the differences in y-axis values.

Tetramorium avium, a ratio of 25:42:33. This ratio can, furthermore, be used to show the degree of any species' affinity to any of the three habitat types sampled. For instance, the carabid Pterostichinae sp. 2 was a forest species (80:19:1), so too was *Metaxinidium nanum* (77:22:1). Harpalinae sp. 3 (57:37:6) and *Crematogaster* sp. 1 (49:43:8) both preferred forest and edge habitat, while Pterostichinae sp. 3 (17:18:65), *Haplotrachelus* sp. 1 (2:10:88), *Pachycondyla peringueyi* (1:28:71), *Meranoplus peringueyi* (0:10:90), *Pheidole* sp. 1 (5:31:64) and *Tetramorium* sp. squaminode-group (1:15:84) all preferred grassland habitat. The ponerine *Pachycondyla wroughtoni* preferred edge and grassland habitats (15:39:46), so too did the doryline, *Dorylus* sp. (1:48:51).

Environmental variables and invertebrate occurrence

Although mean temperature 10 mm above and below ground level did increase into grasslands, these changes were not statistically significant. Surprisingly, relative humidity also did not change significantly across the ecotone. Soil pH decreased significantly from forest to grassland ($F = 2.03$, $p = 0.03$) while percentage soil moisture was significantly higher in grasslands ($F = 20.65$, $p < 0.001$). Percentage organic carbon varied significantly in forests and was significantly lower in grasslands ($F = 2.82$, $p < 0.003$) while soil compaction was significantly lower at the ecotone than both forest and grassland interiors ($F = 2.85$, $p < 0.001$). Both depth of leaf litter ($F = 21.72$, $p < 0.01$) and percentage tree shade ($F = 61.78$, $p < 0.01$) decreased significantly from forest to grassland interior. Percentage ground-cover increased significantly into grasslands ($F = 4.60$, $p < 0.001$) while ground cover height was significantly higher at the ecotone than in either forest or grassland interiors ($F = 7.23$, $p < 0.001$) (Table 3).

Distinct variables contributed to the variability in amphipod, carabid and ant assemblage parameters across the ecotone (Table 4). Soil compaction and relative humidity were the best predictors for amphipod abundance (these variables accounted for 83% of the variation). Carabid abundance related to distance across the ecotone and percentage shade (93% of the variation), while carabid species richness related to soil pH (86% of the variation). Temperature 10 mm above ground level was the best predictor for carabid diversity across the ecotone (44% of the variation). No variable entered the model for ant abundance, while distance across the ecotone, percentage soil moisture and relative humidity were the best predictors of ant species richness (92% of the variation). Ant diversity related to ground cover height, litter depth, percentage organic matter and soil pH (98% of the variation) (Table 4).

Discussion

Ecotones and invertebrates

In human-disturbed landscapes, invertebrates can be more diverse at habitat edges than in habitat interiors. For instance, Helle and Muona (1985) showed that ants, arachnids, gastropods and beetles preferred edge to interior habitats. Similarly, Burkey (1993) found higher ant abundance at neotropical rainforest edges, while Bedford and Usher (1994) showed higher carabid and spider species richness at woodland edges. Social wasps (Hymenoptera: Vespidae) in Brazil showed a preference to forest-savanna edge habitat, both in terms of nesting sites and searching for food (Raw, 1992). The edge was a food-rich environment and provided more prey for the spider species *Nephila clavipes* L. (Vollrath, 1985). This species was not only more abundant at the edge, but was also larger, fed more and grew faster than individuals of the same species in the interior habitat (Vollrath, 1985). Similarly, Fowler *et al.* (1993) showed that invertebrate body size was greater at the forest edge. Didham (1997), reviewing evidence for and against elevated abundance and diversity of invertebrates at forest edges, conclude that invertebrates commonly respond to disturbed habitat edges. Such evidence has in the past led to the suggestion that forests should be subdivided, thereby creating more edge and consequently increasing diversity in the landscape (Mattiske, 1987). All the above-cited studies, however, were in anthropogenically-altered landscapes, and to extrapolate to natural landscapes would

Table 3. Untransformed environmental variables (mean ±1SD) determined across the forest-grassland ecotones.

Variable measured	Forest								Grassland						
	64	32	16	8	4	2	1	E	1	2	4	8	16	32	64
Ta (°C)	16.2	13.2	13.3	15.2	14.9	15.5	15.4	17.5	16.6	17.2	17.9	16.4	17.2	16.7	20.6
SD	6.1	3.8	3.9	5.0	5.3	6.3	5.9	6.9	8.0	9.3	8.4	8.7	9.4	8.2	10.0
Tb (°C)	12.5	10.0	10.3	12.2	12.6	12.3	10.8	13.3	12.4	12.2	13.5	14.5	10.4	11.2	14.8
SD	4.1	2.9	3.1	3.7	4.0	4.7	3.3	4.2	5.9	5.4	6.5	8.2	4.9	5.0	7.4
RH (%)	61.2	62.3	61.6	64.4	64.8	60.5	60.8	60.3	60.2	57.4	63.6	63.8	57.8	59.4	57.4
SD	18.7	18.5	17.0	20.3	21.0	21.4	21.1	21.4	19.1	21.6	22.4	21.0	22.3	20.1	23.0
Soil pH	6.34	5.97	6.09	5.97	5.67	5.59	5.84	5.72	5.63	5.58	5.60	5.37	5.32	5.19	5.25
SD	0.44	0.59	0.51	0.71	0.74	0.56	0.60	0.58	0.52	0.49	0.44	0.28	0.19	0.27	0.14
% Soil moisture	14.5	11.0	11.5	12.4	11.8	14.2	12.8	12.5	11.3	10.7	15.8	23.9	22.1	21.3	20.3
SD	2.2	2.1	0.9	0.9	1.3	2.5	2.1	2.3	1.4	1.1	2.9	2.5	2.6	2.0	3.0
% Organic C	28.7	23.8	26.4	30.2	25.9	30.8	27.8	26.2	24.0	25.5	25.3	25.5	27.2	25.7	30.1
SD	3.1	3.8	1.0	3.0	1.9	1.6	2.8	2.9	3.1	3.4	3.2	3.3	2.3	3.8	2.7
Soil compaction	1.10	1.11	1.15	0.74	0.84	0.80	0.74	0.83	0.88	0.98	0.99	0.98	1.16	1.53	1.41
SD	0.96	0.86	0.94	0.57	0.67	0.59	0.60	0.62	0.66	0.77	0.74	0.66	0.69	1.02	0.78
Leaf litter (mm)	106	89	95	97	82	95	64	96	54	55	58	58	25	19	18
SD	59	36	41	34	52	38	25	25	41	40	45	44	13	11	9
% Tree shade	70.0	67.5	63.1	57.5	57.5	53.8	52.5	41.9	35.0	24.4	11.3	3.8	0	0	0
SD	13.1	15.6	15.8	8.5	11.6	16.4	18.9	15.3	15.1	14.3	14.3	5.8	0	0	0
% Ground cover	66.9	66.7	76.6	75.0	83.1	74.3	79.4	77.3	86.3	87.5	91.3	95.0	98.1	97.5	98.1
SD	25.8	20.2	19.6	16.3	18.1	23.4	12.9	18.9	12.2	13.6	9.2	4.6	2.6	4.6	2.7
GCH* (mm)	372	331	304	258	237	322	321	280	900	607	489	429	288	268	289
SD	154	122	98	80	83	170	166	176	341	488	307	291	99	75	52

Abbreviations: Ta = temperature 10 mm above ground level, Tb = temperature 10 mm below ground level, GCH = ground cover height. Values below forest and grassland headings represent distances (in metres) into that habitat, i.e. the first 64 represents 64 m into forest, while the second 64 represents 64 m into grassland. E = edge.

carry risks for meaningful conservation.

No general edge effect at natural Afromontane forest-grassland edges

In our study there was no significant increase in numbers of carabid and ant individuals or species at the naturally very sharp Afromontane forest edges. Mean carabid abundance and species richness decreased gradually from forest to grassland, while mean ant species richness increased from forest to grassland. No direct biological edge effect (Murica, 1995) was observed. So, although edge effects, in terms of physical and biological changes associated with remnant margins, have a major impact on the ecology of anthropogenically-fragmented tropical (Laurance, 1997) and boreal forests (Spence *et al.*, 1996; Heliola *et al.*, 1999), the same appears not to be true for natural forest patches in the Afromontane region.

Interestingly, the gradual changes in carabid and ant abundance and species richness across the ecotone did not follow the abrupt changes in vegetation architecture from forest to grassland (General Introduction, Fig. 2). Nor did some of the environmental variables. For example, although temperature 10 mm above and below ground level increased from forest to grassland, this change was neither abrupt nor

Table 4. Stepwise variable selection and multiple regression of mean number of amphipod individuals, mean number of carabid and ant individuals and species, and mean carabid and ant diversity (Simpson's diversity index), compared with 12 variables selected across the forest-grassland ecotone.

Assemblage parameter/significant predictors	Coefficients ($P < 0.05$)
Amphipoda	
Individuals; $F_{(2,12)} = 36.35$, $p < 0.001$, $r^2 = 0.83$	
Compaction	-3.389
Relative humidity	-0.075
Carabidae	
Individuals; $F_{(2,12)} = 98.35$, $p < 0.001$, $r^2 = 0.93$	
Distance from the ecotone	-0.079
% Shade	-0.036
Species; $F_{(1,13)} = 89.49$, $p < 0.001$, $r^2 = 0.86$	
pH	17.172
Diversity (Simpson's index); $F_{(1,13)} = 11.80$, $p < 0.005$, $r^2 = 0.44$	
Temperature 10 mm above ground level	75.838
Formicidae	
Individuals	
-	
Species; $F_{(3,11)} = 57.94$, $p < 0.001$, $r^2 = 0.92$	
Distance across the ecotone	0.307
% Moisture	-1.082
Relative humidity	0.126
Diversity (Simpson's index); $F_{(4,10)} = 161.07$, $p < 0.001$, $r^2 = 0.98$	
Ground cover height	-4.173
Litter depth	-2.070
% Organic matter	8.122
pH	-19.209

statistically significant. Also, there was no statistically significant change in relative humidity from forest to grassland, although there may be a biological significance. These results are in sharp contrast to that found at Brazilian Atlantic forest-fragment edges, where air and soil temperature decreased, yet relative humidity increased significantly from farmlands to forest fragments (Stevens and Husband, 1998). Also, small mammal species richness and diversity was significantly explained by distance from the edge; no small mammals were captured in the surrounding farmland (Stevens and Husband, 1998).

Our study, however, differs in one major respect from that of Stevens and Husband (1998). These Afromontane forest sites are not surrounded by agricultural land, but by native grassland, and although fire maintains a sharp transition between forest and grassland, the disturbance (i.e. fire) is a more natural process rather than agricultural. Indeed, although sharp, Afromontane forest-grassland ecotones can be considered natural edges. Kapos *et al.* (1997) argued that modifications in environmental conditions at newly-created edges disappear, or become more complex, as the clear-cut edge matures.

Most environmental variables changed only gradually across the Afromontane forest-grassland ecotone. Exceptions were obvious ones such as percentage soil moisture, percentage tree shade, and ground cover height. These results are in sharp contrast to those found by researchers working in severely-fragmented forest patches (Kapos *et al.*, 1997; Turton and Freiburger, 1997). Furthermore, the findings support our hypothesis that edge effects, also in terms of environmental variables, are less common, albeit potentially more complex, in natural or moderately-disturbed landscapes than in heavily human-disturbed landscapes.

Specific edge effects

Five of the 37 species captured increased in abundance at the ecotone. As mentioned above, the amphipod *T. africana* was notable in this regard. Terrestrial amphipods are active litter decomposers (Friend and Richardson, 1986) breaking down organic matter (Stork and Eggleton, 1992). Soil compaction and relative humidity best predicted mean *T. africana* abundance. Although relative humidity showed little change across the ecotone, soils were less compact at the interface, thereby providing a larger area for life (Giller, 1996). Furthermore, Rendig and Taylor (1989) and Breck and Jenkins (1997) showed that soil hardiness, or soil compaction, negatively affect plant fitness.

The significantly higher abundance of *T. africana* at the ecotone in this study implies high decomposing activities at the boundary. This would contribute to increased nutrient cycling at the edge, and perhaps also reduce fire load. Margules *et al.* (1994) showed that terrestrial amphipods are highly susceptible to anthropogenic disturbance, with a marked decrease in numbers of individuals after fragmentation. Anthropogenic fragmentation of

Afromontane forest can possibly have similar effects on amphipod abundance, which could influence ecosystem processes.

The ant species, *Tetramorium avium*, a seed predator, also showed a marked increase in abundance at the ecotone. Most ant species, however, were more abundant in either forest or grassland habitat. The most striking of these was the ant *Meranoplus peringueyi*, a grassland species. The two most abundant carabid species, Pterostichinae sp. 2 and Harpalinae sp. 3, were forest specialists. It is unclear why Pterostichinae sp. 2 showed such dominance in the carabid assemblage (73.7%). Nevertheless, in other carabid poor systems, such as in grasslands in Melbourne, Australia, Horne (1992) recovered only 15 carabid species of which *Notonomus gravis* (Chaudoir) represented more than 80% of total catch (see New, 1998 for more examples).

Remarkably, none of the ant species occurred only within forests. Also, only *Crematogaster* sp. 1, the most abundant ant species captured, occurred in high numbers in forests, and although high at the edge, was low in the grassland matrix. This aggressive, predacious forest species (Ingham and Samways, 1996) may have been partly responsible for the low ant species richness in forests. In another area of South Africa, Samways (1983, 1990) showed that where a single ant species dominates, overall ant species richness becomes low. His study was, however, in the highly disturbed habitats of commercial orchards, which is characterised by an expected dominance of certain species. Afromontane forests are native habitat, and why a single ant or carabid species dominates is still unclear.

Furthermore, cluster analysis showed that a unique ant assemblage occurred at the interface. This was not because of the occurrence of unique ant species at the forest-grassland boundaries (edge and grassland clusters both sampled equal numbers of species; 21 and 22 species respectively), but rather the marked differences in abundances of certain ant species captured here, compared to either forest or grassland interiors. For example, *Dorylus* sp., *Crematogaster* sp. 1, *Monomorium* sp. 1 monomorium-group and *Tetramorium avium* were abundant at the edges, but also occurred in both forest and grassland interiors, although at low abundances. Also, *Meranoplus peringueyi*, *Pheidole* sp. 1 and *Tetramorium* sp. squaminode-group were abundant in the grassland cluster, but also occurred at forest edges. The forest cluster separated out because only 11 species were captured here, none of which were captured exclusively here (Fig. 5).

Environmental predictors of invertebrates across the ecotone

Different sets of variables predicted amphipod, carabid, and ant assemblage patterns across the forest-grassland ecotone. This is not surprising since the three groups preferred three distinct areas across the ecotone. For instance, the distribution of carabids is sometimes influenced by moisture (Rykken *et al.*, 1997) and on the amount of organic matter on the ground (Van Straalen *et al.*, 1988). Although neither percentage soil moisture nor leaf litter depth predicted carabid abundance or species richness here, grassland soils were, nevertheless, wetter than forest soils, while forests had a significantly deeper litter layer than the grasslands. Grasslands recover quickly after fire and grassland vegetation forms a thick mat of living and dead (standing) material, which possibly entraps moisture between ground and standing vegetation matter. Forest vegetation, on the other hand, uses more soil water, consequently resulting in dryer forest soils, as was observed here. Camargo and Kapos (1995) found that soil moisture was depleted from 40 m - 80 m into an Amazonian forest, arguing that the creation of gaps in the forest increase the variation in microclimate near the ground, and consequently variation in soil moisture. This also appears true for Afromontane forests.

Many ant species construct subterranean nests (Hölldobler and Wilson, 1990) and most variables predicting ant species richness and diversity were associated with soil conditions, as was expected.

Conservation implications

These Afromontane forest patches were surrounded by indigenous grassland where fire maintains a sharp and mature transition between the two ecosystems. Kapos *et al.* (1997) argued that modifications in environmental conditions at newly-created edges disappear, or become more complex, as the clear-cut edge matures. We found little evidence in these old, Afromontane forest-grassland boundaries to support an enhanced biological or abiotic edge effect. We tentatively conclude that edge effects in general may perhaps be more a consequence of human disturbance at edges than of natural factors, except for a few specific, edge species.

Finally, it is important to appreciate the high ant diversity in Afromontane grasslands. Grasslands are often perceived as less valuable than forests, with anthropogenic disturbances such as human settlement, cattle grazing, and afforestation often concentrated in grasslands (Moll, 1976). Indeed, Macdonald (1989) argued that the grassland biome is the most transformed by human activity, in South Africa, and considering that only 2% of this biome is protected (Siegfried, 1992), there is a case for serious concern. These disturbances and threats will continue to influence the character of the Afromontane forest-grassland interface, and ultimately the character of Afromontane forests. In fact, land use by humans has already caused large-scale transformations of the structure and functioning of African ecosystems (Happold, 1995). In terms of conservation priorities, it is vital to conserve grasslands as well as forests if the forest, with its ecotone, is to be conserved intact. Ironically, almost 20 years ago White

(1981) made a strong plea for the preservation of the entire Afromontane region, arguing that the Afromontane flora probably had a more complex origin and evolutionary history than any other in the world. The time has come for such conservation actions.

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Appendix. Amphipod, carabid and ant species and number of individuals captured across the six Afromontane forest-grassland ecotone sites selected.

	Forest								Grassland						
	64	32	16	8	4	2	1	E	1	2	4	8	16	32	64
Amphipoda															
Talistroides africana Griff.	75	108	154	213	467	622	680	728	503	575	281	158	145	102	43
Carabidae															
Harpalinae sp. 1	1	1	1	2	1	1	1	2	3	3	0	1	1	0	1
Harpalinae sp. 3	23	10	8	13	18	7	15	7	12	5	4	0	0	0	3
Pterostichinae sp. 2	304	172	139	144	135	59	56	42	41	17	8	0	1	0	0
Pterostichinae sp. 3	0	4	4	1	0	2	3	2	2	1	8	2	16	5	4
Pterostichinae sp. 4	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Abacillus basilewskyi Strau.	0	0	0	0	0	0	0	0	1	1	0	0	1	2	0
Cophosomorpha caffer Dej.	1	0	0	0	0	0	0	0	0	0	0	1	2	8	0
Haplotrachelus sp. 1	0	0	1	0	1	2	0	0	5	1	9	24	11	28	3
Hystrichopus mnisechi Pèr.	0	0	0	1	0	0	0	0	0	1	4	1	1	2	2
Metaxinidium nanum Basil.	14	5	12	14	11	4	4	6	1	1	1	0	0	0	0
Systolocranius alternans Dej.	0	0	0	0	0	0	0	1	0	0	3	0	1	1	0
Tyronia sp.	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Xenitenus sp.	1	0	1	0	0	0	1	0	0	0	1	0	0	0	0
Number of carabid individuals	346	192	166	175	166	75	80	61	66	30	38	29	34	46	13
Number of carabid species	7	5	7	6	5	6	6	7	8	8	8	5	8	6	5
Formicidae															
Ponerinae															
Streblognathus aethiopicus Smith, 1958	0	0	0	0	1	0	0	0	0	0	0	1	2	6	3
Pachycondyla peringueyi Emery, 1899	0	0	0	0	1	1	6	8	11	9	10	9	23	11	37
Pachycondyla wroughtoni Forel, 1901	0	2	7	0	4	0	6	9	7	11	9	15	13	1	1
Hypoponera transvaalensis Arnold	0	0	0	0	1	1	0	2	0	1	0	0	0	0	0
Leptogenys intermedia Emery, 1902	1	1	0	1	0	6	2	0	0	1	2	2	4	12	6
Anochetus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Dorylinae															
Dorylus sp.	0	0	0	1	4	39	9	126	3	20	189	17	0	1	1
Formicinae															
Camponotus niveosetosus Mayr, 1862	0	1	0	0	0	0	0	1	1	4	8	3	5	7	9
Camponotus sp. foraminosus- group	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Camponotus sp. maculatus- group	0	0	0	0	0	0	0	0	0	0	11	1	0	0	2
Myrmicinae															
Calyptomyrmex clavisetus Santschi, 1914	0	0	0	2	6	9	10	10	3	35	5	0	4	1	0
Crematogaster sp. 1	240	192	213	191	119	231	173	173	170	89	64	30	54	2	9
Crematogaster sp. 2	1	1	8	4	12	13	0	1	0	4	10	1	0	0	0
Monomorium sp. 1 monomorium- group	5	15	23	18	39	49	31	12	24	22	18	22	4	5	21
Monomorium sp. 2 monomorium- group	0	0	0	0	0	2	14	0	0	0	3	8	0	11	9
Meranoplus peringueyi Emery, 1886	0	0	0	0	0	0	4	3	12	27	48	132	159	43	17
Pheidole sp. 1	6	0	0	1	7	8	5	0	56	19	18	0	9	127	24
Rhoptromyrmex n.sp.	0	0	0	0	0	8	0	0	0	1	4	10	13	3	4
Solenopsis punctaticeps Mayr, 1865	0	0	0	0	0	0	1	0	0	0	0	1	3	0	8
Tetramorium avium Bolton, 1980	25	30	44	35	43	54	54	83	71	35	61	66	42	21	37
Tetramorium setigerum Mayr, 1901	0	0	0	0	0	1	0	0	0	0	1	8	2	0	2
Tetramorium sp. simillimum- group	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0
Tetramorium sp. squaminode- group	0	1	0	0	1	1	0	2	7	12	23	28	23	28	25
Number of ant individuals	278	243	295	253	238	423	315	430	366	290	484	355	360	281	216
Number of ant species	6	8	5	8	12	14	12	12	12	15	17	18	15	17	18

Abbreviations: 64 - traps placed at 64 m into forest patches or grassland matrices, 32 - traps placed at 32 m into forest patches or grassland matrices, etc. E - forest-grassland edge.

III

(Manuscript under review)

Inter-seasonal consistency in spatial pattern of invertebrates across a forest patch-grassland matrix ecotone in KwaZulu-Natal, South Africa.

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Abstract

The Afromontane region in the hilly midlands of KwaZulu-Natal, South Africa, is characterised by strong seasonal climatic variation. Summers are hot and wet, while winters are cool and dry. These seasonal differences are expected to reflect on the temporal occurrence of arthropods. Seasonal differences in the distribution patterns of epigaeic amphipods, carabids and ants across a sharp forest-grassland ecotone were investigated using pitfall traps. These invertebrates were sampled continuously across four seasons, summer 1993/4 to spring 1994 inclusive. Invertebrates in general, were more abundant and species rich in spring (September-November) and summer (December-February) than in autumn (March-May) and winter (June-August). Furthermore, for the selected taxa, abundance and species richness patterns across the ecotone did not change inter-seasonally. For example, *Talistroides africana*, the only amphipod species present, was significantly more abundant at the ecotone than in both forest or grassland interiors and this pattern changed little throughout the year. Carabid abundance was significantly higher in the forest and at the ecotone, than in the grassland throughout the year. Ants were significantly more abundant and species rich in the grassland interior than at the edge or deep in the forest for all seasons except winter, during which ant species richness was the same from forest interior to grassland interior. So, although species identities changed from one season to the next, overall inter-seasonal diversity patterns of amphipods, carabids and ants across an Afromontane forest-grassland ecotone were quite consistent.

Introduction

Climate and weather profoundly affect the growth and development of vegetation (Strong *et al.*, 1984). Rainfall seasonality plays a dominant part in plant life through alternating periods of rain and drought (Longman and Jeník, 1992). Furthermore, tropical forest studies show pronounced phenological variation between seasons and/or between years (Van Schaik *et al.*, 1993). Resource availability differs dramatically across seasons with the pattern of resource availability categorised as rapidly increasing, pulsing, steadily renewed, constant, or rapidly decreasing (Price, 1984).

For specialised invertebrates the effects of change in season significantly influence abundance, identities, and numbers of insect species in a community (Wolda, 1983; Strong *et al.*, 1984; Niemelä *et al.*, 1989; 1994). Ants display distinct annual cycling in numbers of individuals and moderate annual cycling in number of species (Samways, 1990b). Not only do species enter and leave the community at different times (Niemelä, 1996), a consequence of resource availability (Strong *et al.*, 1984), but some species, for example some butterflies, display seasonal forms where the dry-season form may be morphologically quite different from the wet-season one (Samways, 1994).

Of particular interest is whether diversity pattern observed in one season is mirrored in other seasons. This is especially so for ecotones which may contain important resources for open country species, especially during dry seasons (Cavalcanti, 1992). Ecotones are areas of transition between adjacent vegetation types. Risser (1995) argued that ecotones intensify, if not control, movement of materials between these vegetation types.

Of additional interest is the identification of true ecotone-dependent species. Kolasa and Zalewski (1995) argued that the identification of an ecotone depends on the time over which interactions of two habitats are observed. Furthermore, as invertebrate assemblages inevitably change over time (Wolda, 1992), it is of interest to know whether a species abundant at the ecotone during one season is also so during the next.

Transition from Afromontane forest to grassland in KwaZulu-Natal, South Africa, is exceptionally abrupt, with a change from forest to grassland often occurring within a few metres (chapter I and II). Afromontane forest-grassland boundaries are naturally sharp, but are also fire maintained (Everard, 1986) with human-induced fires occurring on an almost annual basis.

Here we examine how diversity patterns of epigaeic amphipods, carabids and ants across an Afromontane forest-grassland ecotone change throughout the year. This epigaeic invertebrate assemblage was used because: 1) high invertebrate species richness makes it impossible to sample the entire fauna adequately; 2) many invertebrate groups are insufficiently known taxonomically; and 3) carabids and ants have been shown to be sensitive to changes in habitat, spatially and temporally (Niemelä *et al.*, 1989; Brown, 1991; Kremen *et al.*, 1993; New, 1993; Colwell and Coddington, 1994; Andersen, 1997; chapter I, II).

Since little is known of how ecotonal invertebrate assemblages change over time, we investigated amphipod, carabid and ant diversity patterns across an Afromontane forest-grassland ecotone throughout a year. Specifically, we hypothesise that these taxa will show a shift, in terms of distribution patterns across the ecotone, from one season to the next. A possible explanation for this is that during unfavourable conditions certain species may use the ecotone as a refugia or for resource use (Cavalcanti, 1992), thereby altering distribution patterns across the ecotone.

Study area, materials and methods

Study area and invertebrate sampling

A 25.5 ha natural Afromontane forest patch was selected in the Impendle district, KwaZulu-Natal, South Africa, on the farm Nhlosane (29°35'S 29°58'E) (Chapter II: Fig. 1, site six). Human-induced fires occur almost annually in the Afromontane grassland, usually from mid-August to late September (Van Wilgen *et al.*, 1990). The forest patch selected was dominated by *Podocarpus* tree species and was surrounded by *Themeda triandra* Forssk. dominated grassland. This is apparently a natural situation.

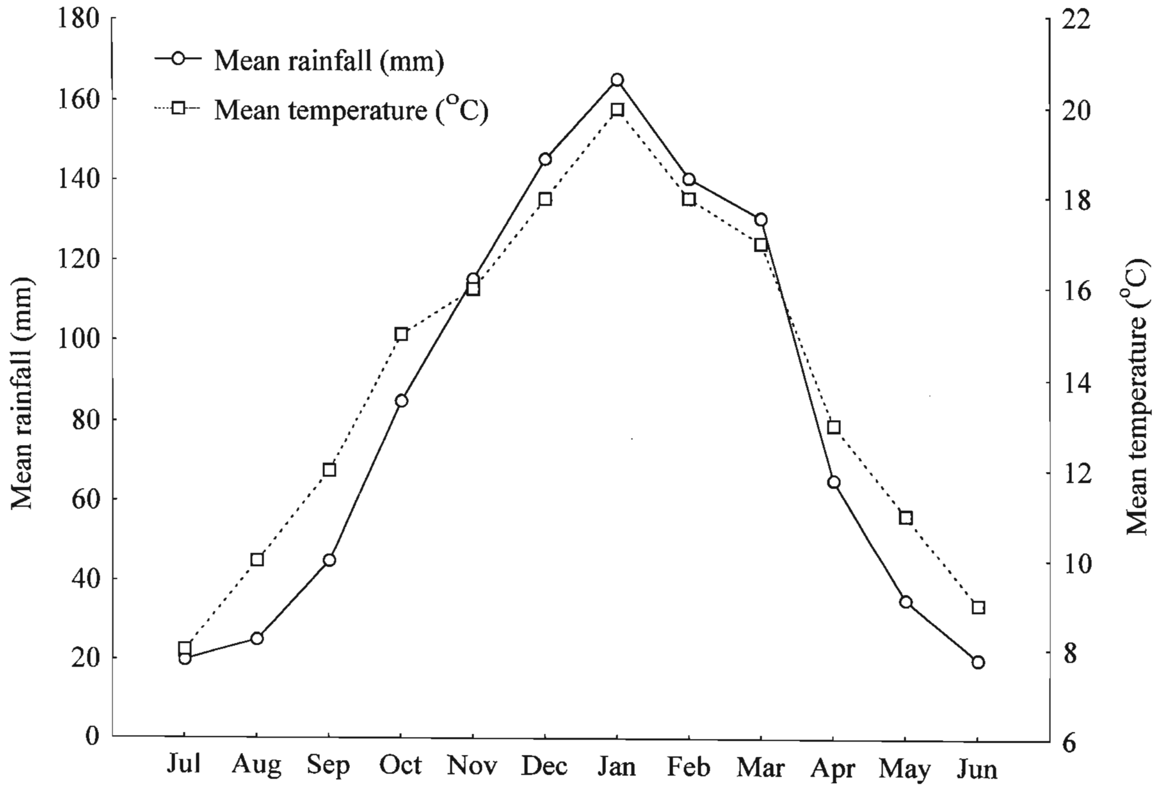

Fig. 1. Mean monthly rainfall (mm) and temperature (°C) for the study area. Data from Schulze (1982) and the Climate Information Office, South African Weather Bureau.

Precipitation is strongly seasonal with much of the rain falling between November and March (highest mean precipitation in January: 165 mm), and a low percentage in winter (lowest mean precipitation in June or July: 20 mm). January is the hottest month (mean monthly temperature: 19-20°C) and July the coldest (mean monthly temperature: 8°C) (Fig. 1) (Schulze, 1982).

Glass-tube pitfall traps (25 mm diameter x 150 mm deep) (Majer, 1978) were used to collect epigaeic invertebrates across the forest-grassland ecotone. One line transect consisted of a trap being placed at the forest-grassland boundary, then at 1, 2, 4, 8, 16, 32, and 64 m into the forest and grassland respectively, resulting in a 128 m transect perpendicular to the boundary. A transect-set consisted of three line transects placed 5 m apart (see chapter II). Transect-sets were replicated five times, and placed 100 m apart to ensure independent sampling (Digweed *et al.*, 1995). Continuous trapping started at the beginning of December 1993 and continued to the end of November 1994, covering four seasons from summer 1993/4 to spring 1994 inclusive. Traps were visited fortnightly, invertebrates removed, and traps refilled with 20 ml of an ethylene-glycerol: alcohol (3:1) mixture. Invertebrates were identified to species where possible.

Statistical analysis

Temporal data were grouped into four seasons: summer 1993/94 (December 1993-February 1994), autumn 1994 (March-May 1994), winter 1994 (June-August 1994), and spring 1994 (September-November 1994). Data were summed per distance across the ecotone, per transect-set, per time of year. This resulted in 15 values per transect-set, i.e. one value per distance across the ecotone. As mentioned above, transect-sets were replicated five times, so statistical analyses were performed on five values per distance, per season. Amphipod abundance, and carabid and ant abundances and species richnesses were transformed to approximate normality to comply with parametric test assumptions (Sokal and Rohlf, 1995). A two-way repeated-measures ANOVA was performed to test for differences in epigaeic invertebrate assemblage parameters across the ecotone, differences in these parameters at different times of the year, and dependence of the effect of time of year on invertebrate distribution pattern across the ecotone.

Cluster analysis was performed to assist in finding natural groupings (Clarke and Warwick, 1994) of samples across the ecotone, and at different times of the year. Here, line transects were divided into five areas, for reasons of simplicity: F (forest-interior; 64 to 16 m inside forest), Fe (forest-edge; 8 to 2 m inside forest), E (edge; 1 m inside forest to 1 m inside grassland), Ge (grassland-edge; 2 to 8 m inside grassland), and G (grassland-interior; 8 to 64 m inside grassland).

An analysis of complementarity was performed on carabid and ant presence/absence data to investigate species identity changes throughout the year. For each taxon, pairs of seasons were compared using:

$$C_{jk} = \left(\frac{\sum_{i=1}^{S_{jk}} | X_{ij} - X_{ik} |}{\sum_{i=1}^{S_{jk}} \max(X_{ij}, X_{ik})} \right) * 100$$

where Xij and Xik are the presence/absence values of species i in species list j and k. Complementarity values vary from 0% (identical species lists) to 100% (no species shared) (Colwell and Coddington, 1994).

Finally, the F:E:G ratio, discussed in chapter II, was used here to identify forest, edge and grassland species.

Results

A total of 2 807 individuals of the amphipod species, *Talistroides africana* (Griff.), was captured. Twenty-three carabid species were captured (2 923 individuals), and 25 ant species were captured (5 945 individuals). Pterostichinae sp. 2 was the most abundant carabid collected (83.6% of total carabid abundance), with Harpalinae sp. 3 the second most abundant species (6.7%). The five most abundant carabid species contributed to 96% of total carabid abundance. *Crematogaster* sp. 1 was the most numerous ant species (40.0% of total ant abundance), *Monomorium* sp. 1 monomorium-group was the second most abundant (14.0%) and *Tetramorium avium* the third most abundant (13.8%). The ten most abundant ant species made up 96% of total ant abundance (Appendix).

Amphipod abundance changed significantly across the ecotone and between seasons (Fig. 2; Table 1). *Talistroides africana* was significantly more abundant at the ecotone except during autumn and winter when abundance was high in the grassland. Moreover, *T. africana* was significantly more abundant in summer than any other season and significantly less abundant in winter than at any other season. Interaction between distance and season was not significant, implying that the spatial distribution of amphipods observed in one season was mirrored in the next.

Carabids were significantly more abundant in forest than in grassland and abundance was significantly different between seasons (Fig. 3; Table 1). Significantly more individuals were captured in spring than any other time of the year. Carabid species richness did not change significantly across the ecotone but did between seasons (Fig. 3; Table 1). Species richness was generally high in the forest and at the edge but low in the grassland. Carabid species richness reflected a seasonal pattern with winter, and to a lesser extent autumn, showing a significantly low richness compared to summer species richness. For carabid abundance, interaction between distance and season was not significant. Again, this implied inter-seasonal consistency in spatial pattern across the ecotone. Carabid species richness pattern across the ecotone was dependent on season of capture.

Ant abundance changed significantly across the ecotone and throughout the year (Fig 4; Table 1). Significantly more individuals were captured in the grassland compared to the forest. Significantly less individuals were captured in winter than any other time of the year, while significantly more individuals were captured in spring than in autumn or winter. Significantly more ant species were captured in the grassland than in the forest (Fig. 4; Table 1). Also, significantly less ant species were captured in winter than any other time of the year, while significantly more species were captured in summer than in any other season. Although ant abundance across the ecotone was season-independent, ant species richness pattern across the ecotone depended on time of year of capture.

Carabid cluster analysis showed little pattern both in terms of distance or season grouping (Fig. 5A). In fact, beetle composition differs substantially between habitat types and seasons. Ant assemblage, however, divided into four distinct clusters (Fig. 5B). A grassland-interior group separated at 53% similarity (G in Fig. 5B). Three distinct groups formed at 67% similarity; two of which included all forest-interior (F) and forest-edge (Fe) samples; and a

Table 1. Two-way repeated measures ANOVA for distance across an Afromontane forest-grassland ecotone over four seasons (from summer 1993/4 to spring 1994), for number of amphipod individuals and number of carabid and ant individuals and species.

Assemblage parameter and factor	df	MS	df error	MS error	F	p
Amphipoda						
Individuals						
Distance	14	4.391	60	0.846	5.190	< 0.001
Season	3	10.132	180	0.246	41.210	< 0.001
Distance*Season	42	0.343	180	0.246	1.393	= 0.072ns
Carabidae						
Individuals						
Distance	14	2.824	60	0.361	7.834	< 0.001
Season	3	3.678	180	0.066	55.337	< 0.001
Distance*Season	42	0.077	180	0.066	1.157	= 0.255ns
Species						
Distance	14	7.121	60	9.522	0.748	= 0.718ns
Season	3	170.092	180	1.926	88.319	< 0.001
Distance*Season	42	2.991	180	1.926	1.553	= 0.026
Formicidae						
Individuals						
Distance	14	6.482	60	1.810	3.581	< 0.001
Season	3	26.089	180	0.734	35.522	< 0.001
Distance*Season	42	0.632	180	0.734	0.860	= 0.712
Species						
Distance	14	0.202	60	0.054	3.759	< 0.001
Season	3	1.939	180	0.020	95.355	< 0.001
Distance*Season	42	0.054	180	0.020	2.660	< 0.001

Data were transformed to approximate normality when necessary. df = degrees of freedom, MS = mean square, ns = not significant.

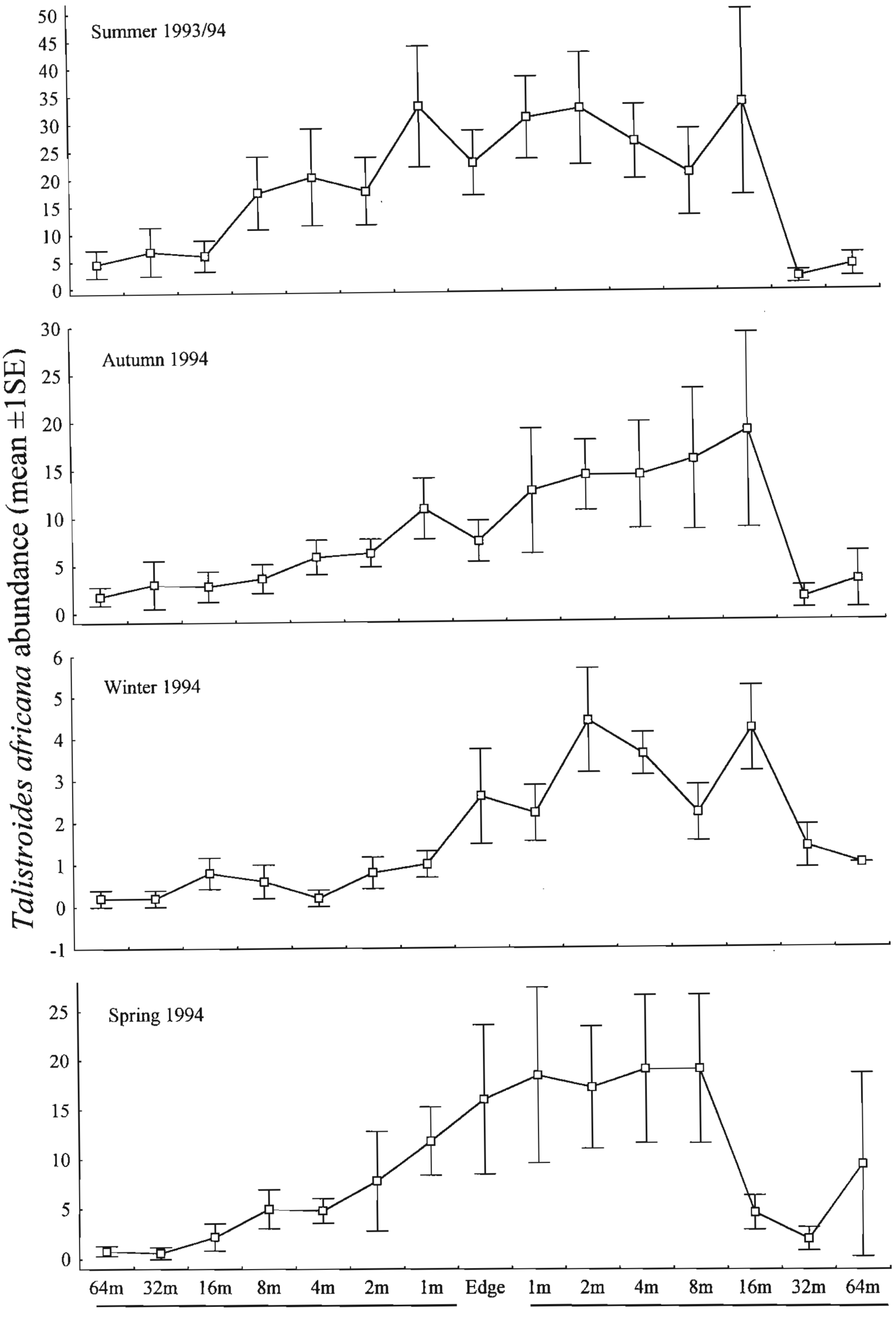

Fig. 2. Mean (±1SE of mean) *Talistroides africana* abundance across an Afromontane forest-grassland ecotone, throughout the year. Means were calculated from sums of the five transect-sets per distance treatment (see text). Please note the different scales of the planes.

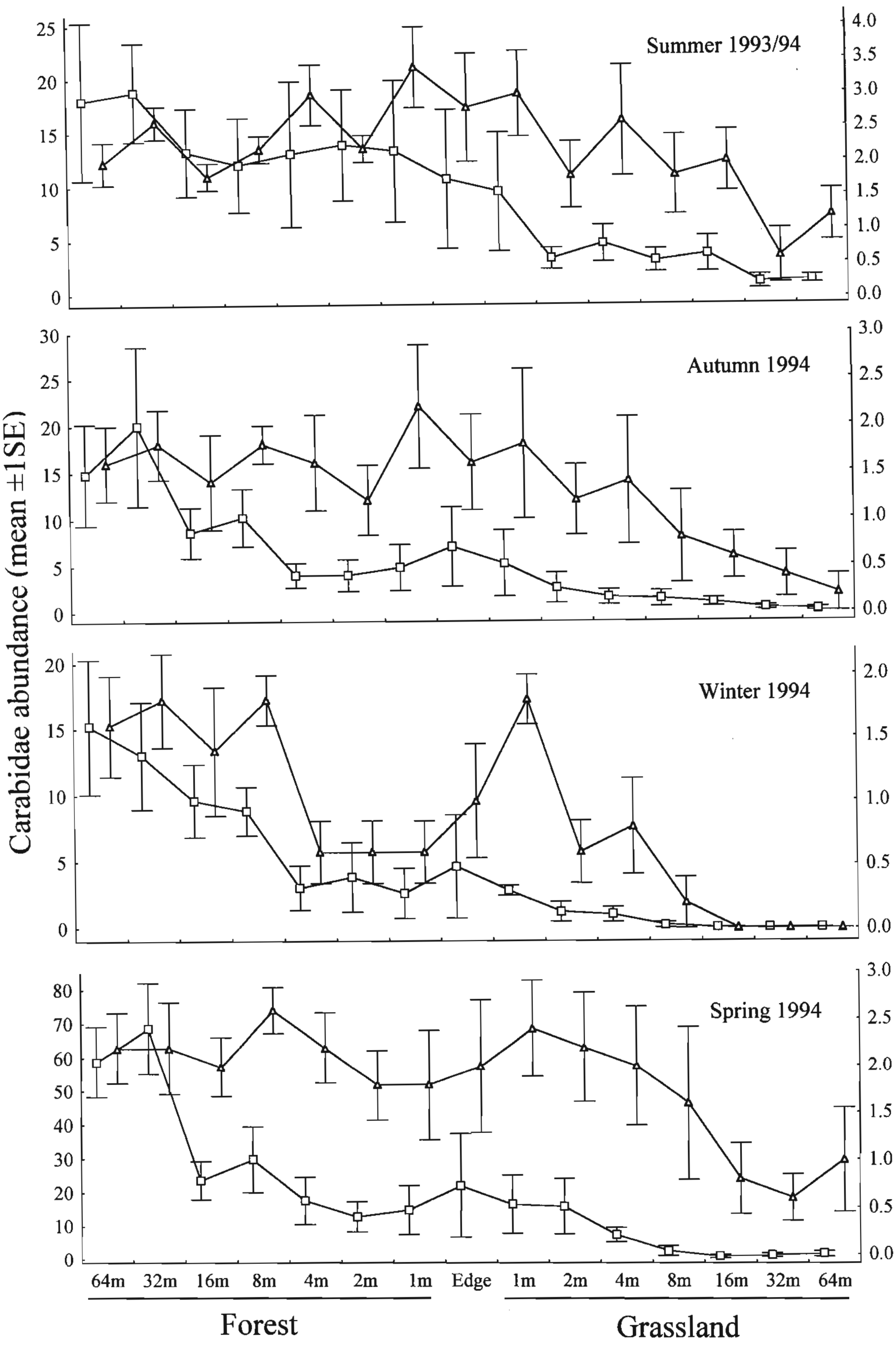

Fig. 3. Mean (±1SE of mean) carabid abundance (□) and species richness (△) across an Afromontane forest-grassland ecotone, throughout the year. Means were calculated from sums of the five transect-sets per distance treatment (see text). Please note the different scales of the panels.

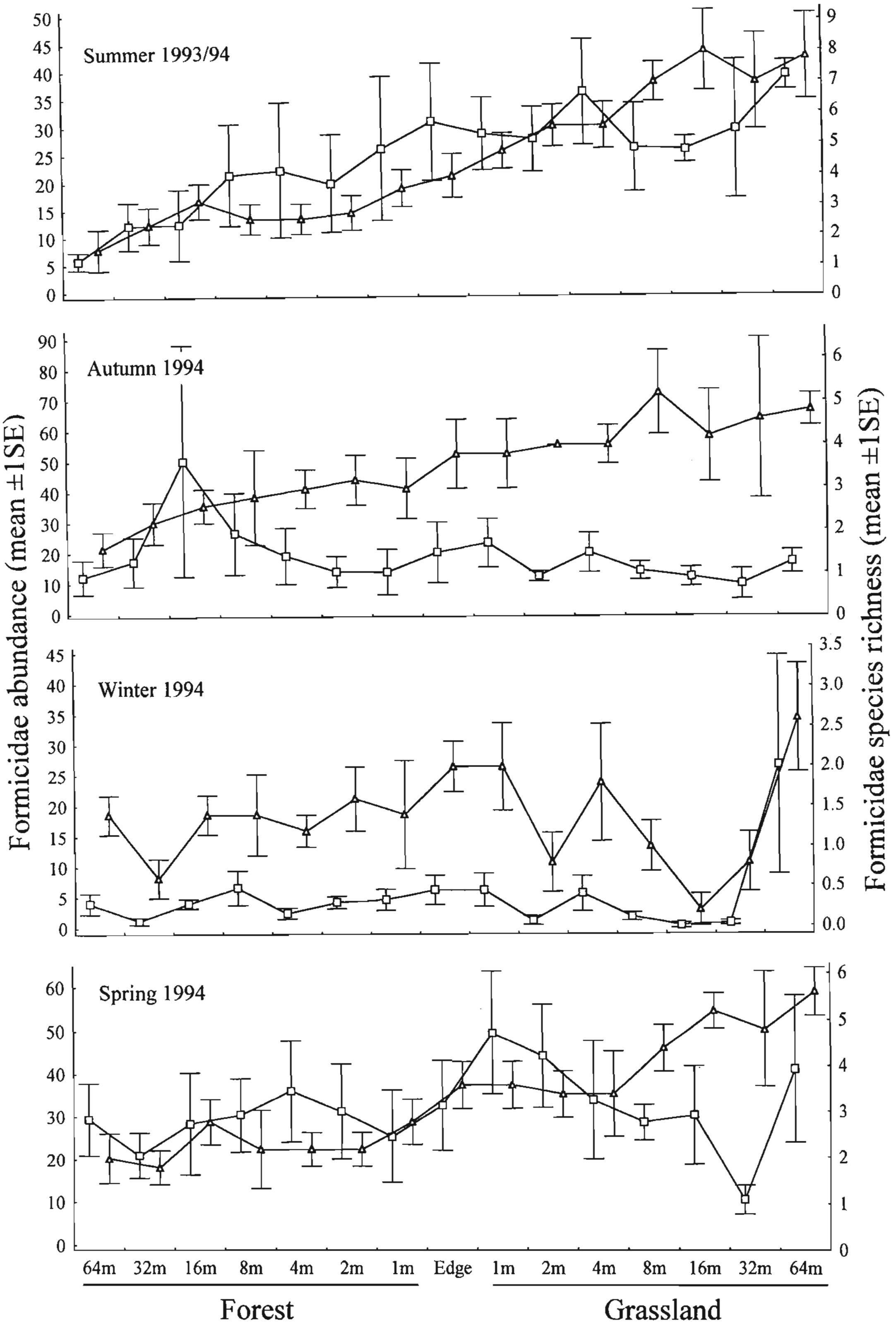

Fig. 4. Mean (±1SE of mean) ant abundance (□) and species richness (△) across an Afromontane forest-grassland ecotone, throughout the year. Means were calculated from sums of the five transect-sets per distance treatment (see text). Please note the different scales of the panels.

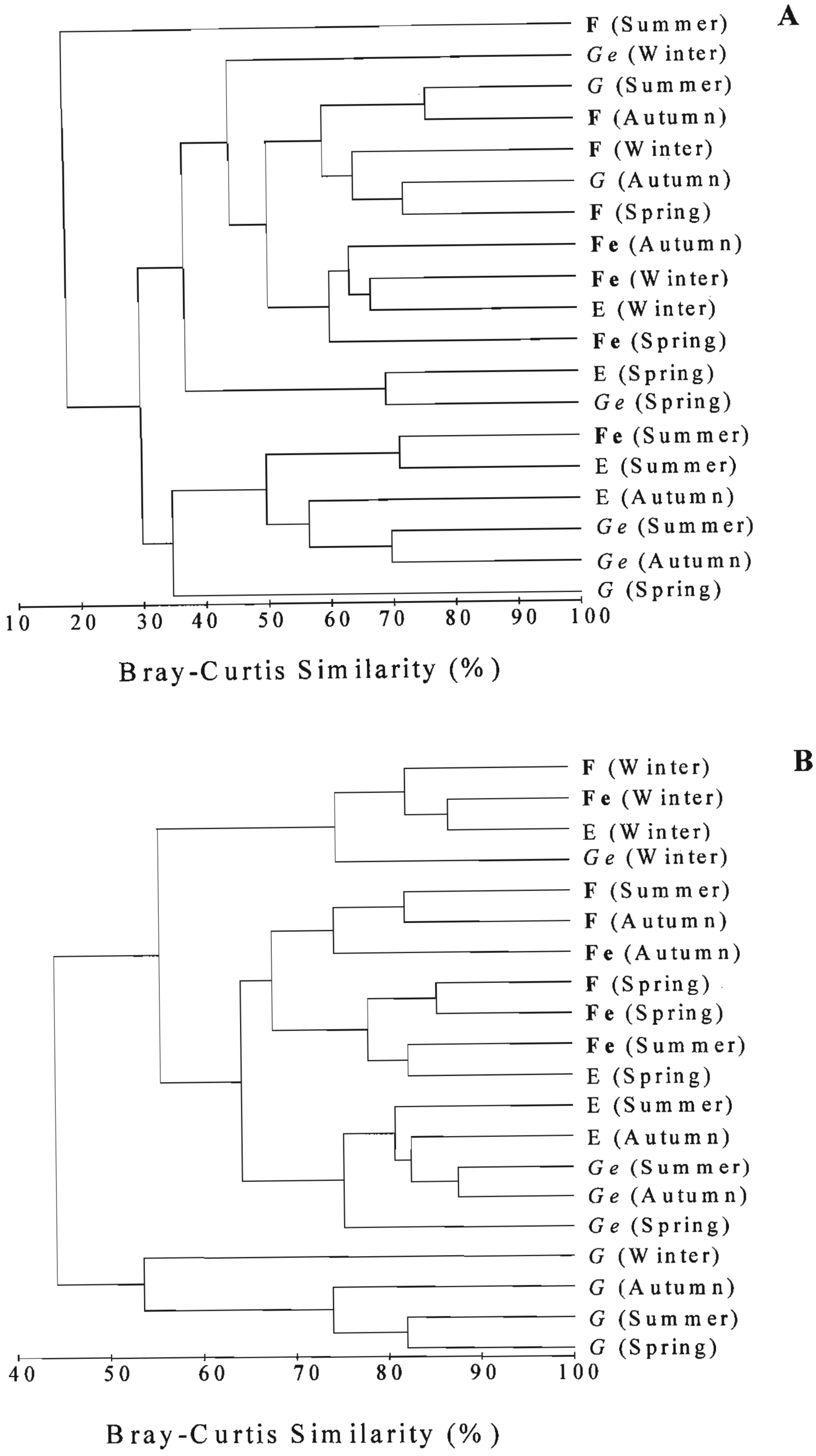

Fig. 5. Dendogram of hierarchical clustering of distances across the Afromontane forest-grassland ecotone and between seasons, based on the Bray-Curtis similarity matrices created for carabids (A) and ants (B). Abbreviations: **F** (traps from 64-16 m inside forest), **Fe** (from 8-2 m inside forest), E (from 1 m inside forest to 1 m inside grassland), *Ge* (from 2-8 m inside grassland), and *G* (from 16-64 m inside grassland).

third with most of the edge (E) and grassland-edge (Ge) samples.

Analysis of complementarity (Table 2) indicated that winter shared few carabid species with other seasons. Perhaps this was because only five carabid species were captured in winter. Many species were shared between spring, summer and autumn. Most species were shared between autumn and spring, while the least between summer and winter. Harpalinae sp. 3, Pterostichinae sp. 2 and *Metaxinidium nanum* occurred in all four seasons. Nine carabid species only occurred in a single season, while five species; Harpalinae sp. 1, Pterostichinae sp. 3, *Abacillus basilewskyi*, *Cyrrtomoscelis ferrugimoides* and *Haplotrachelus* sp. 1 were present in each season except winter (Appendix). For ants, complementarity values were lower than for carabids, i.e. more species were shared between seasons. Few ant species were shared between winter and any other season (again mainly because winter was species poor), but many between summer, autumn and spring. Twelve ant species were present in all four seasons, while five species were present only in a single season. Also, five ant species; *Streblognathus aethiopicus*, *Leptogenys intermedia*, *Dorylus* sp., *Pheidole* sp. 1 and *Tetramorium* sp. squaminode-group were absent from winter but present in all other seasons (Appendix).

Table 2. Complementarity (%) between seasons, for both carabids and ants. Values after complementarity values (in parentheses), represent number of species in common. Values after seasons (in parentheses) represent total number of species captured for that season.

	Summer	Autumn	Winter
Carabidae			
Summer (18)	-		
Autumn (14)	54.6 (10)	-	
Winter (5)	85.0 (3)	73.3 (4)	-
Spring (12)	50.0 (10)	37.5 (10)	69.2 (4)
Formicidae			
Summer (20)	-		
Autumn (22)	17.4 (19)	-	
Winter (13)	35.0 (13)	47.8 (12)	-
Spring (20)	18.2 (18)	32.0 (17)	35.0 (13)

Discussion

Only a single Afromontane forest-grassland site was sampled here, therefore our results are not applicable at regional or landscape levels, but only at the local, individual site.

The Afromontane region in KwaZulu-Natal, South Africa, is characterised by strong seasonality (Schulze, 1982; South African Weather Bureau), with highest temperatures coinciding with highest rainfall (December to February). Winter months (June to August) are relatively cold and receive little rain (Moll, 1968). The amphipod, carabids and ants showed significant responses to this seasonal variation. Abundances and species richnesses were low in winter, while significantly higher in the wet and warm summer and spring months. Many populations show regular annual cycling, while others, particularly many insects, are characterised by low levels and occasional outbreaks (Samways, 1990b).

Spatial pattern: differences across the ecotone

Although carabid and ant abundance and species richness changed substantially with season, the proportion of individuals and species between interiors and edge remained the same. Similarly, the amphipod *Talistroides africana* was significantly more abundant at the ecotone (F:E:G ratio, 16:48:36, see chapter II for F:E:G ratio explanation), except in autumn and winter when its numbers were very low. This result concurs with what was found elsewhere (chapter II) in that *T. africana* is a true ecotone species. Carabid overall abundance and species richness was always low in this grassland site compared to that at the edge and in the forest. Ant overall abundance and species richness always increased significantly from forest to grassland.

Although carabid assemblage-structure (illustrated by cluster analysis) across the ecotone was without clear pattern, ant assemblage-structure clearly changed from forest to grassland. This result is significant for conservation decisions in the Afromontane region. Not only were ants more species rich in the grassland, but the grassland also harboured a considerably different ant assemblage than that at the edge and in the forest. Grasslands are usually perceived as less valuable than forest, with anthropogenic disturbances such as human settlement, cattle grazing, fire, and afforestation often concentrated in grasslands (Moll, 1976). Nevertheless, grasslands harboured a unique ant assemblage, not only during one part of the year, but throughout a one-year period.

Results here showed that native grasslands in the Afromontane region warrant more attention in conservation decisions (Matthews *et al.*, 1993), since many ant species (here 12 ant species), and other grassland species like some grasshoppers (Samways, 1990a) and hemipterans, occur only here. In fact, Meadows and Linder (1989) have argued that grasslands, rather than the forests, must have been the long-standing component of the Afromontane vegetation mosaic, the true relict community of the Afromontane region. This argument is given credence by the high percentage endemic species in the grasslands compared to the few narrowly distributed endemics in the so-called undifferentiated Afromontane forest component (Matthews *et al.*, 1993).

Again, as in chapter II, none of the ant species captured was restricted to the forest patch. And only *Crematogaster* sp. 1 (F:E:G ratio, 41:42:17), the most abundant ant species captured, occurred in abundance in the forest (chapter II, F:E:G ratio = 49:43:8). This species was also present at the edge and in the grassland (very low numbers in the grassland-interior). This aggressive, predacious species was perhaps partly responsible for the low ant species richness in the forest patch because where single ant species dominates, local ant species richness tends to be low (Samways, 1983, 1990b). *Crematogaster* species, apart from being predacious, also feed on honeydew produced by homopteran species and are arboreal, therefore somewhat restricted to forested areas (Ingham and Samways, 1996). Furthermore, they are rare in grasslands as was shown here.

Using the F:E:G ratio (see chapter II), two ant species, *Monomorium* sp. 1 monomorium-group (33:46:21) (chapter II, 32:45:23), and *Tetramorium avium* (21:57:22) (chapter II, 25:42:33) preferred edge habitat. The identification of edge species is difficult since intraspecific use of the edge, or ecotone, varies with time of year (Yahner, 1988), but here ecotone species could be identified since sampling was continuous over a 12-month period. These two ant species appeared to be true edge species since their respective abundances were high at the ecotone during all seasons, except winter when abundances for many species were low.

Except for Harpalinae sp. 3, Pterostichinae spp. 2 and 3, and *Metaxinidium nanum*, most carabids occurred at very low abundances indeed. The high abundance of Pterostichinae sp. 2, a forest species (F:E:G = 72:27:1) (chapter II, 80:19:1) overshadowed carabid abundance pattern across the forest-grassland ecotone. Nevertheless, many carabids still occurred across the ecotone, although at very low numbers, and contributed to the diversity here. *Metaxinidium nanum* (54:42:4) (chapter II, 77:22:1) was another species more abundant in the forest, while Harpalinae sp. 3 (38:47:14) (chapter II, 57:37:6) occurred in abundance at the interface area and Pterostichinae sp. 3 (4:43:53) (chapter II, 17:18:65) was confined to the edge and grassland.

Temporal pattern: differences between seasons

Talistroides africana, an active litter decomposer (Friend and Richardson, 1986) showed regular seasonal cycling with significantly more individuals captured during warmer seasons than colder ones. Climate, and not resource availability, is probably responsible for this significant decrease in *T. africana* numbers in winter. The reason could be the high monthly total litter and leaf fall in winter months, documented in a similar southern-hemisphere, warm temperate forest (Wirminghaus, 1990). Also, main fruiting peak of forest trees occurs during the dry winter months (Wirminghaus, 1990). So, despite there being much litter on the forest floor during winter, i.e. high resource availability, *T. africana* abundance and activity was low.

In autumn and winter, *T. africana* was more abundant in grassland adjacent to the edge. This result was unexpected since grasslands in the Afromontane region are dry during these seasons while amphipods require a relatively moist environment since they are susceptible to desiccation (Friend and Richardson, 1986, Margules *et al.*, 1994). One possible explanation is that in this zone, from the edge up to 16 m into the grassland, the amphipod escapes predation from organisms using the edge as a refugium during autumn and winter months. This would, however, require that they move between habitats, a statement for which there are no data available as of yet. Another explanation is simply that there are differences in predation rates between forests, edges and grasslands. For example, scorpions are more abundant at the edge in winter (Ingham and Samways, 1996) and they may prey on the amphipods, lowering their abundance here. Also, few carabid and ant individuals, which are potential predators, were captured in this zone (edge to 16 m into the grassland) during autumn and winter.

Carabid abundance patterns across the ecotone was season-independent. In other words, the general abundance pattern observed in one season was mirrored in any one of the other seasons. Nevertheless, carabid abundance and species richness were significantly higher in summer and spring than in autumn and winter. But, unlike the situation in cold-temperature areas (Lindroth, 1985, 1986), several carabid species in this study were active as adults in winter. One species, Pterostichinae sp. 1 even appeared in traps only in winter. These winter species tended to avoid the grassland interior, which is very dry and highly prone to fires at this time (Schulze, 1982; Van Wilgen *et al.*, 1990). Indeed, no carabids at all were captured from 16 to 64 m into the grassland during winter.

Ant richness was significantly lower in winter than at other times of the year. In winter, unlike the situation in the other three seasons, there was no general increase in ant species richness into the grassland. In winter, ants were species richer at both the ecotone and in the forest. This was the result of a change in ant composition in winter, with many specific grassland species being present in spring, summer and autumn, but absent in winter. Forest and edge species (e.g. *Crematogaster* sp. 1, *Monomorium* sp. 1 monomorium-group, and *Tetramorium avium*) that were abundant in spring, summer and autumn were also present in winter, but not abundantly.

Ant species turnover throughout the year was considerably lower than that of carabids. This is perhaps not surprising since these two groups follow different life strategies. Carabids are solitary organisms, while ants occur in social groups (Hölldobler and Wilson, 1990; Lövei and Sunderland, 1996), and these strategies are possibly partly responsible for the difference in seasonal occurrence. In carabids, high adult activity coincides with the reproductive period (Thiele, 1977; Niemelä *et al.*, 1989). Although we did not study this aspect, we suspect that this is the case for carabids in our study area too.

Ant colonies can be more active over longer periods of time, and are usually more permanent features in a particular habitat, while different carabid species are active at different times of the year (Lindroth, 1985, 1986; Niemelä *et al.*, 1989). Also, many ant species feed on honeydew and seeds, or can scavenge, activities that can, to some extent, be performed throughout the year.

Summary

Kolasa and Zalewski (1995) argued that the identification of edge species depends on the time over which interactions of two habitats are observed. This is perhaps true over short time periods, i.e. days or even weeks, when ecotones are frequently hotter and drier than habitat interiors (Turner and Corlett, 1996). Or over long time periods, i.e. decades and longer, when habitats, and consequently ecotones, move due to large-scale climatic variability (Hopkins, 1992; Kershaw, 1992). On an annual basis however, amphipods, carabids and ants showed little change in distributional pattern across an Afromontane ecotone. In other words, *T. africana*, an obvious ecotone species, was most abundant at the edge not only during summer, but also in spring, autumn and winter. Also, carabid species richness was high in the forest and at the edge and low in the grassland throughout the year, while ants were almost always more species rich in the grassland than in the forest. Thus, in general, amphipod, carabid and ant abundance and species richness patterns across this Afromontane forest-grassland boundary appear to be seasonally-independent, at least over a one year time period.

To conclude, amphipod, carabid, and ant assemblages singly and collectively tracked changes in season. Wolda (1983, 1992) has shown that, even in the tropics, invertebrate assemblage-structure changes with season. Indeed, amphipod, carabid, and ant assemblages in the subtropical study here singly and collectively changed substantially in abundance with season. For many invertebrate taxa, e.g. carabid beetles and spiders, seasonal occurrence is well known in the northern hemisphere (e.g. Niemelä *et al.*, 1989; 1994), but this is one of the first studies documenting the seasonal occurrence of several invertebrate taxa in South Africa.

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Appendix. Total numbers of amphipod individuals, and carabid and ant individuals per species captured over a 12-month period, from December 1993 to November 1994.

	1993	1994										
	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov
Amphipoda												
Talistroides africana Griff.	603	453	323	291	248	69	48	29	50	61	295	337
Carabidae												
Harpalinae sp. 1	1	0	1	1	0	0	0	0	0	2	5	3
Harpalinae sp. 3	39	36	14	18	5	1	1	0	2	17	28	35
Harpalinae sp. 4	0	1	0	1	0	0	0	0	0	0	0	0
Pterostichinae sp. 1	0	0	0	0	0	0	2	2	0	0	0	0
Pterostichinae sp. 2	297	128	68	124	167	66	53	54	196	288	555	448
Pterostichinae sp. 3	13	9	16	9	1	0	0	0	0	0	5	5
Pterostichinae sp. 4	0	1	0	0	0	0	0	0	0	0	0	0
Abacillus basilewskyi Strau.	7	1	0	1	0	0	0	0	0	0	2	5
Aristopus decorus Strau.	1	0	0	1	1	1	0	0	0	0	0	0
Cophosomorpha angulicollis Strau.	0	1	0	0	0	0	0	0	0	0	0	0
Cyrrtomoscelis ferrugimoides Strau.	3	0	5	4	0	0	0	0	0	2	0	5
Haplotrachelus sp. 1	11	5	7	2	0	0	0	0	0	0	6	11
Hystrichopus mnisechi Pèr.	2	2	0	0	0	0	0	0	0	0	0	0
Hystrichopus praedator Pèr.	0	0	0	1	0	0	0	0	0	0	0	0
Hystrichopus vigilans Sturui.	0	0	1	0	0	0	0	0	0	0	0	0
Hystrichopus sp.	0	0	2	0	0	0	0	0	0	0	0	0
Metaxinidium nanum Basil.	4	2	2	0	5	7	4	0	9	12	14	6
Metaxinidium sp.	0	0	0	2	3	5	3	0	3	1	3	5
Microlestes sp.	0	2	0	0	0	0	0	0	0	1	2	2
Systolocranius alternans Dej.	5	2	1	0	0	0	0	0	0	0	1	2
Tyronia sp. 1	0	0	0	1	1	0	0	0	0	0	1	0
Xenitenus sp.	0	0	0	0	1	0	0	0	0	0	0	0
Unknown sp.	3	0	0	0	0	0	0	0	0	0	0	0
Number of carabid individuals	386	190	117	165	184	80	63	56	210	323	622	527
Number of carabid species	12	12	10	12	8	5	5	2	4	7	11	11
Formicidae												
Ponerinae												
Streblognathus aethiopicus Smith, 1958	1	1	0	2	0	0	0	0	0	0	0	2
Pachycondyla wroughtoni Forel, 1901	72	32	42	45	41	12	3	1	1	3	17	41
Pachycondyla peringueyi Emery, 1899	7	2	5	2	2	1	0	0	1	1	3	1
Hypoponera transvaalensis Arnold	0	0	0	0	1	0	0	0	0	0	0	0
Leptogenys intermedia Emery, 1902	16	12	10	6	3	0	0	0	0	5	10	9
Anochetus sp.	1	0	0	0	0	0	1	0	0	0	3	1
Dorylinae												
Dorylus sp.	41	21	2	64	202	0	0	0	0	0	3	27
Formicinae												
Camponotus niveosetosus Mayr, 1862	1	2	2	3	1	0	1	0	3	2	9	14
Lepisiota sp.	5	1	6	1	1	0	0	0	1	1	1	1
Plagiolepis sp. 2	0	0	0	0	0	0	0	0	0	0	3	8
Myrmicinae												
Calyptomyrmex clavisetus Santschi, 1914	2	4	10	7	3	0	0	1	0	1	3	4
Crematogaster sp. 1	227	215	124	85	154	183	67	34	66	296	540	384
Crematogaster sp. 2	21	15	16	23	34	33	10	21	87	14	39	51

Appendix. *(continued)*

	1993	1994										
	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov
Monomorium sp. 1 monomorium-group	81	46	61	82	48	33	7	5	38	103	182	147
Monomorium sp. 2 monomorium-group	2	6	5	2	1	5	0	1	1	9	18	13
Myrmicaria pallida Arnold, 1925	0	0	0	1	1	0	0	0	0	0	0	0
Pheidole sp. 1	25	42	23	3	10	0	0	0	0	0	2	5
Rhoptromyrmex n.sp	44	48	63	40	27	1	1	0	1	39	50	32
Solenopsis punctaticeps Mayr, 1865	0	0	2	2	4	0	0	0	0	0	0	0
Strumigenys sp.	0	0	0	2	0	0	0	0	0	0	0	0
Tetramorium avium Bolton, 1980	183	136	73	113	78	13	12	6	8	36	70	94
Tetramorium setigerum Mayr, 1901	1	3	0	0	2	0	0	0	1	0	8	9
Tetramorium sp. simillimum-group	1	4	1	0	1	0	0	0	0	0	0	0
Tetramorium sp. squaminode-group	13	17	16	12	2	3	0	0	0	1	17	25
Cerapachyinae												
Cerapachys wroughtoni Forel, 1910	0	0	0	0	0	0	0	0	0	0	1	1
Number of ant individuals	2737	607	461	495	616	284	2096	69	208	511	979	869
Number of ant species	19	18	17	19	20	9	8	7	11	13	19	20

IV

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Invertebrate conservation at the interface between the grassland matrix and natural Afromontane forest fragments

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Abstract. Diversity patterns of amphipods, carabid beetles and ants were investigated in five naturally-fragmented Afromontane forest remnants, and in the surrounding grassland matrix. Forests were architecturally similar. In contrast, grasslands surrounding these forests are subject to great differences in anthropogenic impacts. Consequently, transition from forest to grassland ranged from being abrupt (heavy disturbance) to gradual (little disturbance). Significantly different mean numbers of carabid individuals and species were captured between sites and multivariate analyses showed clear separation in carabid assemblage-structure with level of disturbance. Carabids were, furthermore, significantly more diverse in forests, compared to grasslands. Ants, however, were equally species rich between sites but were significantly more abundant and species rich in grasslands than forests. Amphipods, represented here by a single species, *Talistroides africana*, was significantly less abundant at highly disturbed sites and significantly more abundant in forests than grasslands. Results support the hypothesis that the dynamics of remnants are influenced by their surrounding landscape. Here, the dynamics of amphipods and carabids (predominantly forest taxa) were influenced by different disturbance regimes in grasslands surrounding these forests. Epigaeic ants, a predominantly grassland taxon here, also showed significant differences in assemblage-composition between sites with varying disturbance. Conserving Afromontane grasslands should be of prime concern because this will include the protection of forest/grassland ecotones and forest remnants.

Key words: Afromontane forests, ecotone, epigaeic invertebrates, grassland matrix, invertebrate conservation

Introduction

Anthropogenically altered landscapes characteristically consist of isolated natural habitat patches, surrounded by farm fields, cropland and human settlement (Stevens and Husband 1998). These isolated, natural habitats have, and still are, experiencing varying degrees of human pressures, ranging from complete destruction, to moderate levels of disturbance at their edges. Although evident that humans have greatly impacted natural systems by fragmentation and isolation, exactly what impacts these processes have on animal assemblages, particularly invertebrates, are poorly understood (Didham 1997). Of particular interest are the possible effects of matrix vegetation on the dynamics of invertebrates inside forest patches (Saunders et al. 1991), and the effects of forest edges, which become a dominant feature of heavily fragmented landscapes (Jagomägi et al. 1988; Laurance 1997), on invertebrate assemblages. Forest–grassland mosaics in the southern African Afromontane region provide a good opportunity to study these interests.

Afromontane forests and grasslands have been influenced by similar climatic fluctuations (Geldenhuys and Knight 1989; Lawes 1990). Although some suggest that forest covered most of the Afromontane region in the past (McCracken 1986), palaeobotanical and archaeological data suggest that the grassland biome has existed for at least a 1000 years (Ellery and Mentis 1992). Since 1870, forests in KwaZulu-Natal have been logged extensively (McCracken 1986). Today however, many of the larger Afromontane forests are protected, while forests on private land is often seen as an asset. Nevertheless, bark stripping (Cooper 1985), removal of trees for firewood and selective logging still take place. The greatest impact on this forest–grassland mosaic, however, is to the grassland, which is burnt annually to promote new growth for cattle farming, and destroyed by afforestation of exotic tree species (Moll 1976).

The unusual Afromontane forest–grassland mosaic pattern, where small patches of forest dot an extensive grassland matrix, is not the result of forest reduction and destruction by humans, but existed long before a significant number of humans arrived in the area (Meadows and Linder 1989). In terms of this mosaic pattern, the greatest threat is to forest margins, which are important for the survival of these forests (Moll 1969; Geldenhuys and MacDevette 1989). These margins, or ecotones, contain compositional and structural characteristics of both adjacent habitats, as well as distinctive microhabitats specific to the ecotone (Risser 1995). Additionally, ecotones frequently contain relatively high levels of biodiversity, and often have a complex vegetation architecture (Murcia 1995; Risser 1995).

Little is known about diversity patterns of invertebrates in the KwaZulu-Natal Afromontane region. Invertebrates are small, 'hyperdiverse', sensitive to environmental variability, and are therefore good indicators of habitat heterogeneity, ecosystem diversity, and environmental stress (Dempster 1991; Colwell and Coddington 1994; Weaver 1995; McGeoch 1998). Among these invertebrates, carabids (Carabidae) and ants (Formicidae) have been identified as sensitive indicator taxa in natural and disturbed systems (Majer 1983; Brown 1991; Stork and Eggleton 1992; Andersen 1991, 1997). Carabids and ants are used here to investigate diversity patterns across five Afromontane forest/grassland ecotones. Sites vary greatly in type and intensity of grassland disturbance, and we tested whether the dynamics of invertebrates in forest patches are driven by factors arising in the surrounding landscape (Saunders et al. 1991).

Materials and methods

Study area and sampling design

Five forest patches were selected in KwaZulu-Natal, South Africa (Figure 1). These forests are *Podocarpus* spp. dominated, while *Themeda triandra* Forssk. is the dominant grass species in the surrounding grasslands (Acocks 1988). Such mistbelt *Podocarpus* forests cover an area of 30,868 ha, mainly in the 'forest belt' region, east of the Drakensberg mountains (Cooper 1985). They are often on cool and moist south or south-east facing mountain slopes (McCracken 1986). Grasslands show little structural variation (Meadows and Linder 1989). Forest patches vary in size but were otherwise similar in altitude, mean temperatures and rainfall, and in having strong seasonality (Table 1).

The Ngeli site had transitional vegetation up to about 25 m into the grassland. The Blinkwater and Karkloof sites had sharp edges, where transition from forest to grassland occurred within a metre. The Dargle and Enon sites were characterised by sharp edges, but unlike Ngeli, Blinkwater and Karkloof, grassland matrices showed

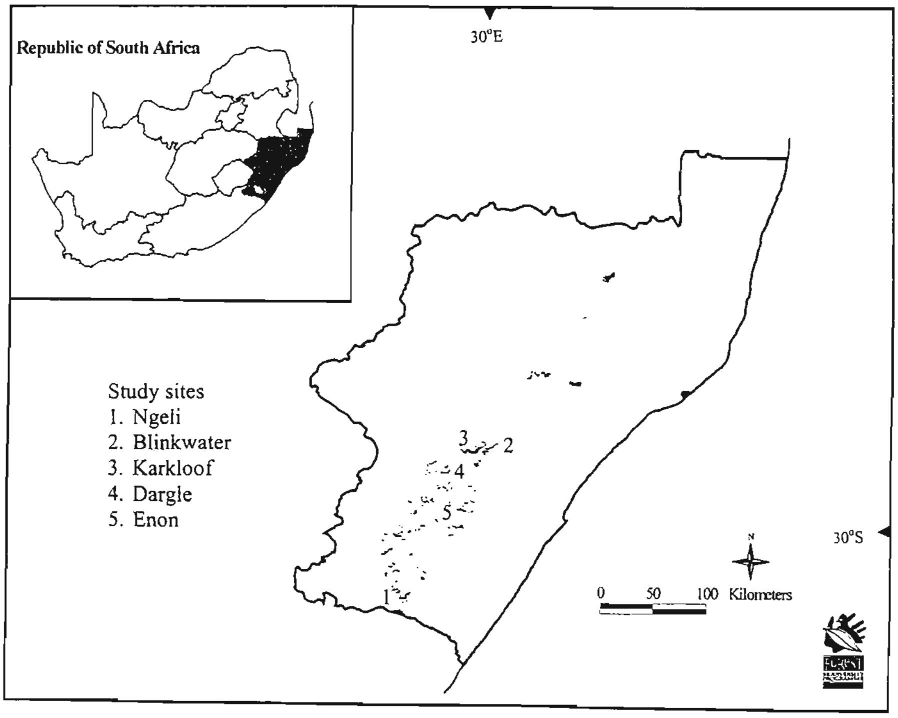


Figure 1. Location of study sites in KwaZulu-Natal, South Africa. 1 – Ngeli, 2 – Blinkwater, 3 – Karkloof, 4 – Dargle, and 5 – Enon. Map was created by the Forestry Biodiversity Programme, University of Natal, Pietermaritzburg.

Table 1. Study site characteristics (data from Cooper (1985) and Schulze (1982)).

Characteristics	Site 1 (Ngeli)	Site 2 (Blinkwater)	Site 3 (Karkloof)	Site 4 (Dargle)	Site 5 (Enon)
Disturbance gradient	Undisturbed	→	→	→	Heavily disturbed
Forest patch size in hectares[a]	715 (752)	325 (1081)	441 (2899)	97 (194)	625 (625)
Location	30°31′17″S 29°41′14″E	29°14′15″S 30°28′03″E	29°18′28″S 30°12′49″E	29°28′48″S 30°00′00″E	29°47′20″S 30°10′32″E
Site altitude (m a.s.l)	1540	1460	1400	1380	1260
Mean annual precipitation (mm)	1000–1200	900–1000	1000–1200	900–1000	900–1000
Highest mean precipitation (mm)	150–170	140–150	160–170	140–160	130–160
(month)	(Dec–Jan)	(Dec–Jan)	(Dec–Jan)	(Dec–Jan)	(Dec–Feb)
Lowest mean precipitation (mm)	10–20	10–20	10–20	10–20	10–20
(month)	(Jun–Jul)	(Jun–Jul)	(Jun–Jul)	(Jun–Jul)	(Jun–Jul)
Seasonality index (precipitation)[b]	40–45%	45–50%	45–50%	45–50%	40–45%
Mean annual temperature	14–15 °C	15–16 °C	14–15 °C	15–16 °C	14–15 °C
Highest mean temperature	20 °C	19–20 °C	19–20 °C	19–20 °C	19–20 °C
(month)	(Jan)	(Jan)	(Jan–Feb)	(Dec–Feb)	(Jan–Feb)
Lowest mean temperature	10–11 °C	10–11 °C	9–11 °C	10–11 °C	9–11 °C
(month)	(Jun)	(Jun–Jul)	(Jun–Jul)	(Jun–Jul)	(Jun)

[a] Values in parentheses represent the local forest complex sizes according to Cooper (1985). The values preceding them represent the sizes of forest patches sampled in this study.

[b] Seasonality index: A 100% means that all precipitation occurs in one month, while 0% indicates that precipitation is the same for each month. The values here indicates strong seasonality throughout the region.

high levels of disturbance from annual fires and heavy grazing. Sites were classed according to level of disturbance, from least disturbed, site 1 to most disturbed, site 5 (Ngeli < Blinkwater = Karkloof < Dargle < Enon) (Table 1).

Carabids and ants were collected using glass pitfall traps (diameter = 25 mm, length = 150 mm) (Majer 1978). In addition, *Talistroides africana* Griff., the only amphipod species present in the area was also sampled. Twenty millilitres of an alcohol-glycerol mixture (3:1) was poured in the traps, and traps were checked fortnightly from December 1995 to the end of March 1996 (South African summer).

Five traps, 10 m apart, were placed at 128, 32, 8, and 2 m inside the forest, at the boundary, and at 2, 8, 32 and 128 m into the grassland. This resulted in a 45-trap, 256 m line transect-set, perpendicular to the forest/grassland boundary, at each site. Invertebrates collected were identified to species level wherever possible.

Statistical analyses

A species accumulation curve was constructed for the cumulative number of carabid and ant species captured. Pitfall trap order was randomised 100 times to eliminate heterogeneity among sampled units, and the mean and standard deviation of $S(n)$ (number of species discovered) computed for each value of n between 1 and 225 (Colwell and Coddington 1994). The total number of carabid and ant species in the community (S^*) were estimated using:

$$S^* = S/(1 - p_0),$$

where p_0 represents the number of unsampled species in the community (Magurran 1988), i.e. the species to the left of the veil line (Preston 1962).

Non-metric multidimensional scaling (NMDS) ordination, using a Bray-Curtis triangular similarity matrix, was used to construct a two-dimensional map of carabid and ant assemblages. Data were $\sqrt{}\sqrt{}$-transformed, i.e. downweighting the effects of common species. NMDS ordinations use ranks of the similarities between samples. This is an appealing and generally applicable base from which to build a graphical representation of the sample patterns, since the ordination presents relative values of similarity (ranks), i.e. more similar samples are plotted closer together, while dissimilar samples are indicated further apart (Clarke and Warwick 1994). An analysis of similarity (ANOSIM) identified significant differences between paired sites (Clarke and Warwick 1994) for both carabids and ants.

An analysis of complementarity was performed on presence/absence data for both carabids and ants. For each group, pairs of sites were compared using:

$$c_{jk} = \left(\frac{\sum_{i=1}^{S_{jk}} |X_{ij} - X_{ik}|}{\sum_{i=1}^{S_{jk}} \max(X_{ij}, X_{ik})} \right) * 100$$

where X_{ij} and X_{ik} are the presence/absence values of species i in species list j and k. Complementarity values vary from 0% (identical species lists) to 100% (no species shared) (Colwell and Coddington 1994).

A two-level nested analysis of variance (Sokal and Rohlf 1995) was used to test for differences among sites, since we were mainly interested in the variance in amphipod, carabid and ant abundances and species richnesses among sites, and secondly, in differences explained by the variation between different distances across the ecotone. ANOVA data were transformed to approximate normality to comply with parametric assumptions (Clarke and Warwick 1994).

In addition, Simpson's diversity index was calculated at each sampling station. This index reflects the probability that any two individuals drawn at random from a population will belong to the same species (Ludwig and Reynolds 1988), and an increase in the reciprocal form (1/D) reflects increase in diversity (Magurran 1988; New et al. 1996). Whittaker's measure (β_W) was used to calculate turnover, or β-diversity across site ecotones:

$$\beta_W = S/(\alpha - 1),$$

where S = total number of species recorded in the system, and α = the average sample diversity where each sample is of standard size and diversity is measured as species richness (Magurran 1988). β-diversity, across the ecotone, was graphically presented through hierarchical cluster analysis (group-average linking algorithm with Bray-Curtis similarity metric). Cluster analysis aims to find 'natural groupings' of samples such that samples within a group are more similar to each other than samples in different groups (Clarke and Warwick 1994).

Finally, population dynamics of abundant species were investigated by plotting their distribution patterns across the ecotone.

Results

Assemblage-structure at all sites combined

One amphipod, 30 carabid and 46 ant species were collected, with a total of 7749, 984, and 8148 individuals captured, respectively (Appendix). The ant species accumulation curve reached an asymptote after 225 pooled pitfall trap samples (Figure 2), suggesting that most ant species present at the sites, were captured. More effort is, however, needed to capture all carabid species (Figure 2). The truncated lognormal distribution estimated totals of 47 ant and 34 carabid species.

Hystrichopus vigilans was the most abundant carabid species (21.2% of total carabid abundance) with almost twice as many individuals captured than the second most abundant carabid, *Abacillus basilewskyi* (Figure 3). *Tetramorium avium* was the most abundant ant species (35.9% of total ant abundance) with more than three times as many individuals captured than the second most abundant ant, *Anoplolepsis custodiens* (Figure 3). Eleven carabid (36.7%) and six ant (13.0%) species were represented by less than five individuals.

Differences in assemblage-structure between sites

Carabid and ant assemblage-structures differed significantly between sites. For carabids, Dargle and Enon (heavily disturbed sites) were significantly different in assemblage-structure from one another, and from the other sites (Figure 4; Table 2), while Blinkwater and Karkloof (moderately disturbed sites) showed no significant difference in assemblage-structure. Although ant assemblage-structure showed significant differences among sites, the pattern was more complex. Again Blinkwater and Karkloof showed no significant differences in assemblage-structure, neither did Karlkoof and Enon (Figure 4; Table 2).

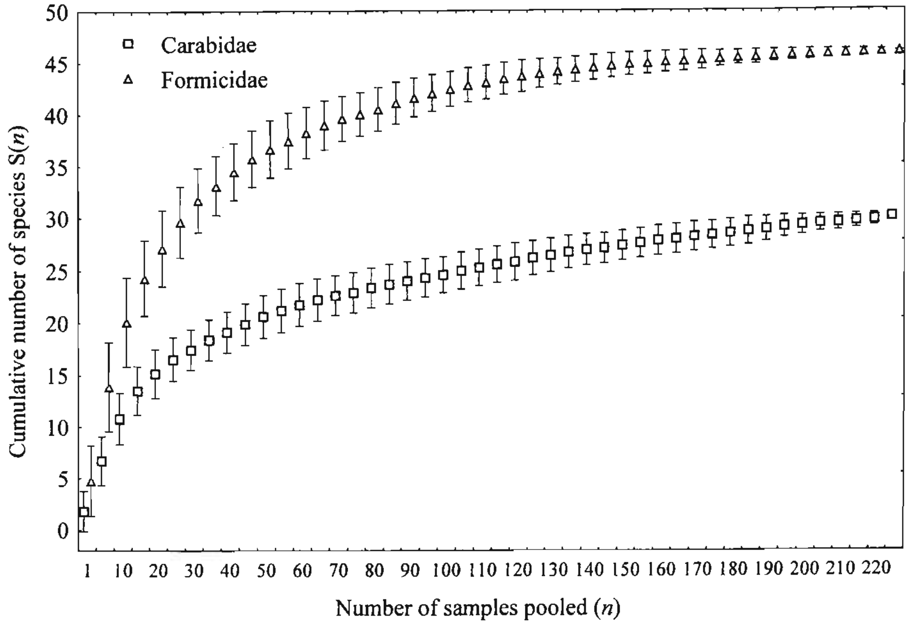


Figure 2. Carabidae and Formicidae accumulation curves from 225 pitfall traps. Each point represents the mean of 100 randomisations of sample pooling order and error bars are the corresponding standard deviations.

Blinkwater shared many carabid species with Ngeli and Karkloof, and Karkloof shared many species with Ngeli. The other site combinations shared few species (Table 3). Ant complementarity percentages were generally lower than that of carabids, i.e. sharing more species between sites. For ants, Enon shared most species with Blinkwater and many with Ngeli and Karkloof (Table 3).

Significantly different mean numbers of amphipod, carabid and ant individuals were captured between sites (Table 4). For both amphipods and carabids, significantly higher numbers of individuals, and species (Carabidae only), were captured at the least disturbed sites (Ngeli, Blinkwater and Karkloof), than at the highly disturbed sites (Dargle and Enon). Surprisingly, the most disturbed site (Enon) yielded a high ant abundance and Karkloof, a relatively undisturbed site, yielded a low ant abundance. Lowest ant abundance was, again at a highly disturbed site (Dargle). Mean ant species richness did not change significantly among sites. Both carabid and ant diversities were highest at the least disturbed site (Ngeli), and lowest at the highly disturbed site (Enon) (Table 5).

Changes in assemblage-structure across ecotones

Significantly different mean numbers of carabid and ant individuals and species were captured across all the forest/grassland ecotones combined (Figure 5; Table 4).

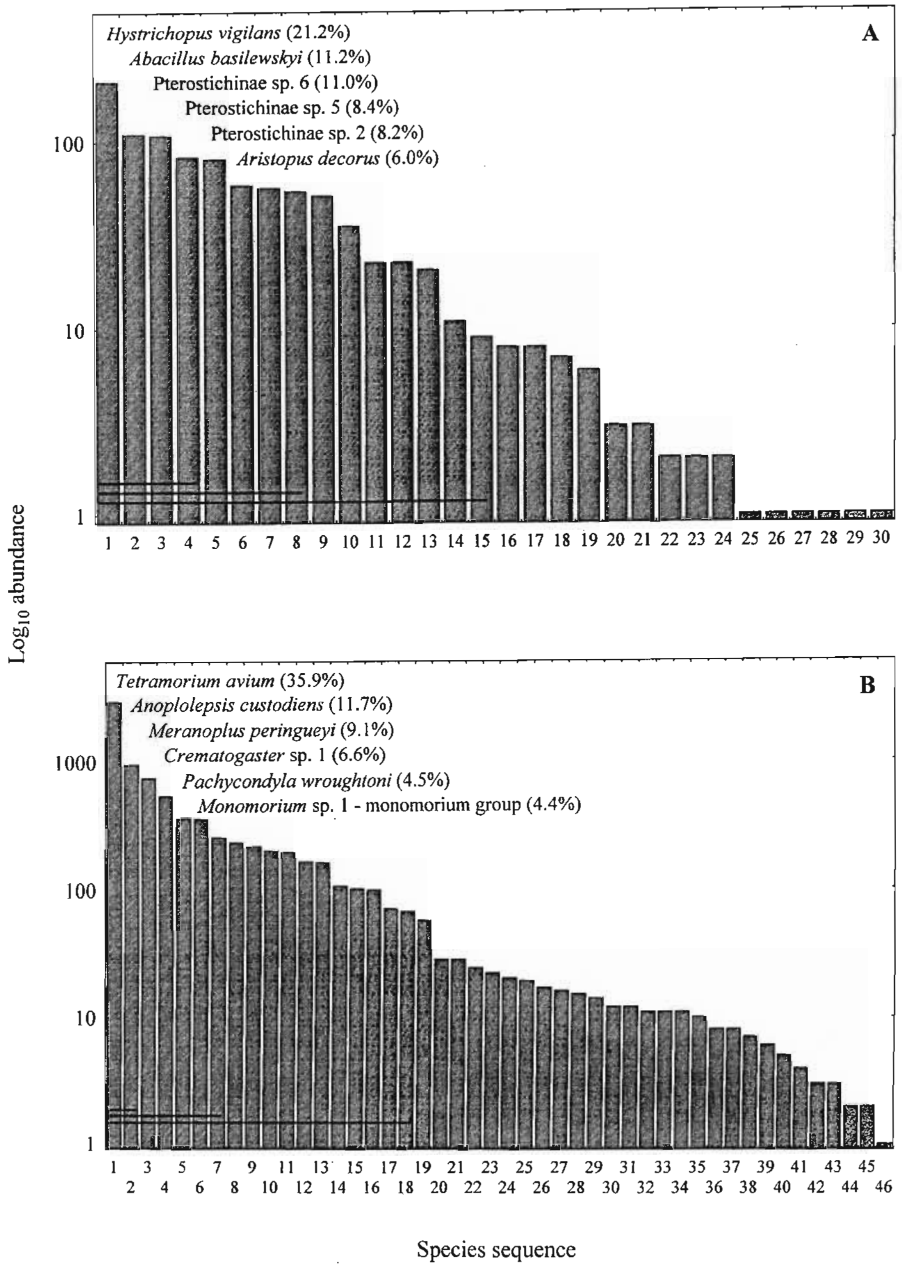
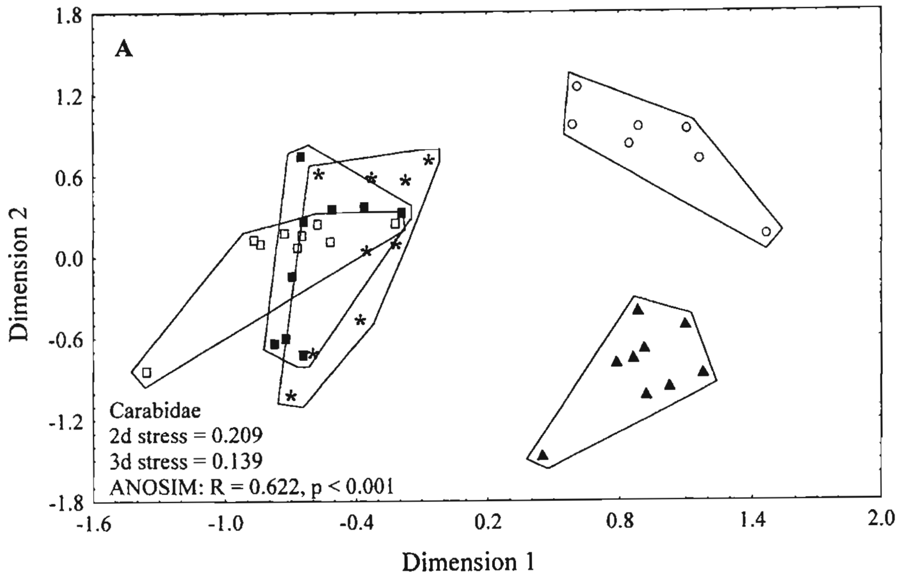


Figure 3. Rank abundance plots (A – Carabidae, B – Formicidae) illustrating the abundance of each species on a logarithmic scale against the species' rank, in order from most abundant to least abundant species. Species making up 50%, 75% and 95% of total abundance are presented by the three horizontal lines, and the six most abundant species (and their percentages) are given.



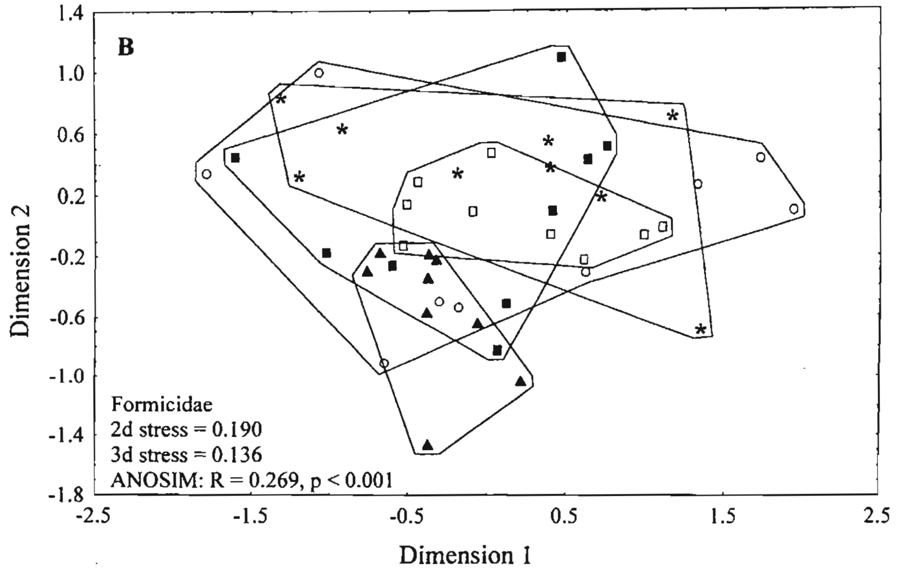


Figure 4. Non-metric multidimensional scaling ordinations for Carabidae (A) and Formicidae (B) at the five sites selected. Symbol explanations: □ – Ngeli, ∗ – Blinkwater, ■ – Karkloof, ▲ – Dargle, and ○ – Enon. Stress values, ANOSIM *R* statistic and *P* values are also given.

Table 2. ANOSIM pairwise comparisons (R statistic) of sites using the Bray–Curtis similarity matrix produced for Carabidae (lower triangular) and Formicidae (upper triangular).

Site	Site 1 (Ngeli)	Site 2 (Blinkwater)	Site 3 (Karkloof)	Site 4 (Dargle)	Site 5 (Enon)
Ngeli	–	0.314**	0.274*	0.430**	0.148*
Blinkwater	0.476**	–	0.155 ns	0.500**	0.181*
Karkloof	0.350**	0.011 ns	–	0.367**	0.106 ns
Dargle	0.897**	0.814**	0.838**	–	0.254**
Enon	0.821**	0.624**	0.745**	0.755**	–

$* = P < 0.05$; $** = P < 0.005$.

The significance levels were not adjusted to allow for multiple comparisons, since no such constructs were possible here. Comparisons with P-values close to 0.05 should be interpreted with caution.

Amphipod abundance, and carabid abundance and species richness decreased significantly at the boundary and into the grassland. However, ants showed a significant increase in numbers of individuals and species into the grassland (Figure 5). While carabid diversity decreased from forest to grassland, ant diversity increased (Table 5).

Carabid and ant β-diversity was highest at Enon, i.e. few species were shared across the ecotone, and lowest at Ngeli, i.e. sharing many species across the gradient (Table 5). β-diversity across the ecotone was graphically presented using cluster analysis. Carabids divided into three distinct clusters, a forest cluster (traps placed at 128 m into forests to the edges), a cluster immediately outside the forests (traps at 2 to 8 m into grasslands), and a grassland interior cluster (traps at 32 to 128 m into grasslands) (Figure 6). Ants also divided into three distinct clusters, a forest interior cluster (traps from 128 to 8 m into forests), a forest edge cluster (traps at 2 m inside

Table 3. Complementarity of Carabidae (lower triangular) and Formicidae (upper triangular) species between the five study sites selected. Complementarity values range from 0 (identical species lists) to 100 (no species shared).

Site (S)	Site 1 (24)** (Ngeli)	Site 2 (28) (Blinkwater)	Site 3 (27) (Karkloof)	Site 4 (15) (Dargle)	Site 5 (30) (Enon)
Ngeli	–	51.4	54.3	65.5	45.7
(15)*		(17)	(16)	(10)	(19)
Blinkwater	45.0	–	51.4	73.5	38.9
(16)	(11)		(18)	(9)	(22)
Karkloof	33.3	36.8	–	68.8	45.9
(15)	(12)	(12)		(10)	(20)
Dargle	87.5	83.3	87.5	–	71.4
(12)	(3)	(4)	(3)		(10)
Enon	82.4	83.3	82.4	93.8	–
(5)	(3)	(3)	(3)	(1)	

S = total number of species captured at that site, * Carabidae, ** Formicidae. Values in parentheses, below complementarity values, are the numbers of species shared in that comparison.

Table 4. Nested analysis of variance showing differences between mean numbers of individuals and species per study area, and per distance across the forest/grassland ecotone, for Amphipoda, Carabidae and Formicidae.

Invertebrate group	Source of variation	df	SS	F	*P*
Individuals[a]					
Amphipoda	Among patches	4	82.76	5.604	<0.002
	Among distances across the ecotone	40	147.69	10.857	<0.001
	Error	180	61.22		
Carabidae	Among patches	4	34.72	9.939	<0.001
	Among distances across the ecotone	40	34.93	3.928	<0.001
	Error	180	40.02		
Formicidae	Among patches	4	16.05	5.167	<0.002
	Among distances across the ecotone	40	31.06	7.474	<0.001
	Error	180	18.70		
Species[a]					
Carabidae	Among patches	4	47.89	12.358	<0.001
	Among distances across the ecotone	40	38.76	3.816	<0.001
	Error	180	45.71		
Formicidae	Among patches	4	13.43	1.554	0.205 ns
	Among distances across the ecotone	40	86.46	15.837	<0.001
	Error	180	24.57		

[a] Data were transformed to approximate normality when necessary. SS = sums of squares, ns = not significant.

forests and at edges), and a grassland cluster (traps from 2 to 128 m into grasslands) (Figure 6).

Finally, species showing preference for forest, ecotone or grassland were identified (Figure 7). *Talistroides africana* and *T. avium* both showed clear preference for forests. So did *H. vigilans*, Pterostichinae sp. 5 and *Aristopus decorus*, but at lower abundances. *Abacillus basilewskyi*, and Pterostichinae spp. 2 and 6 showed increase in numbers at the ecotone. *Anoplolepsis custodiens* and *Meranoplus peringueyi* both showed clear preference for grasslands, and *Monomorium* sp. 1 – monomorium group, *Pheidole* sp. 1 and *Crematogaster* sp. 2 also showed preference for grasslands, although at lower abundances. *Crematogaster* sp. 1 and *Pachycondyla wroughtoni* both showed preference for ecotones.

Discussion

Changes in carabid diversity

Afromontane grasslands appeared to be a non-preferred environment for almost all carabids. Significantly lower numbers of individuals and species were captured there, and species diversity decreased across the gradient from forest interior to grassland interior. Furthermore, none of the six most abundant carabid species showed a clear preference for grasslands. Carabid species lists for the Afromontane region are,

Table 5. Simpson's diversity index (given as $1/D$) at the five study sites, and across the forest/grassland ecotone, for Carabidae and Formicidae. Whittaker's measure (β_W) was used to calculate turnover, or β-diversity, across site ecotones.

	Carabidae		Formicidae		Whittaker's diversity measure	
Site	$\bar{Y}$	SD	$\bar{Y}$	SD	Carabidae	Formicidae
Ngeli	5.12	1.52	4.66	3.39	1.11	1.16
Blinkwater	3.52	1.48	2.61	1.72	2.13	1.65
Karkloof	3.33	1.50	3.85	1.54	2.00	1.70
Dargle	3.39	2.61	4.05	1.36	2.09	1.21
Enon	3.08	0.63	2.70	1.29	2.46	2.55

	Forest (m from edge)					Grassland (m from edge)			
Taxon	128 m	32 m	8 m	2 m	Edge	2 m	8 m	32 m	128 m
Carabidae									
$\bar{Y}$	5.44	3.58	5.27	3.53	3.23	3.23	4.27	2.92	2.10
SD	0.80	1.19	2.69	2.30	0.98	1.86	2.03	1.16	0.85
Formicidae									
$\bar{Y}$	1.55	2.37	2.31	3.20	3.35	5.22	5.24	4.70	4.25
SD	0.64	1.66	1.43	1.47	1.07	2.02	3.22	1.74	1.93

$\bar{Y}$ = mean, SD = standard deviation.

however, incomplete and therefore subject to sampling error (Colwell and Coddington 1994).

Although sampling size was equal among sites, greater effort is needed to give a full picture of individual species' range and occupancy here, particularly for rare species. Nevertheless, many common carabids displayed disjunct distributions among sites, and it is possible that for some local reasons, such as demographic and environmental factors (Saccheri et al. 1998), these species may have become temporarily extinct at the disturbed sites. Here we may have a situation possibly involving metapopulation dynamics, but Hanski and Simberloff (1997) have warned against automatically applying metapopulation models, since research on exact local extinction and migration rates, and how these are affected by patch size and isolation, are required (Hanski et al. 1995). Sampling a larger number of forest patches and sampling over a number of years may reveal whether species occur in metapopulations here, as was shown by Saccheri et al. (1998) for butterflies on the Åland islands, Finland.

Although insufficiently replicated (only five sites), differences in carabid diversity and assemblage-composition can cautiously be explained by differences in level of local disturbances at the sites. Although forests were relatively undisturbed, the grassland matrix surrounding these forests showed marked differences in anthropogenic exploitation. The relatively undisturbed site (Ngeli, Blinkwater and Karkloof) grasslands experienced moderate levels of disturbance, mainly from fire, while the disturbed site (Dargle and Enon) grasslands showed heavy exploitation, being close to human settlement and showing evidence of frequent fire and heavy cattle grazing.

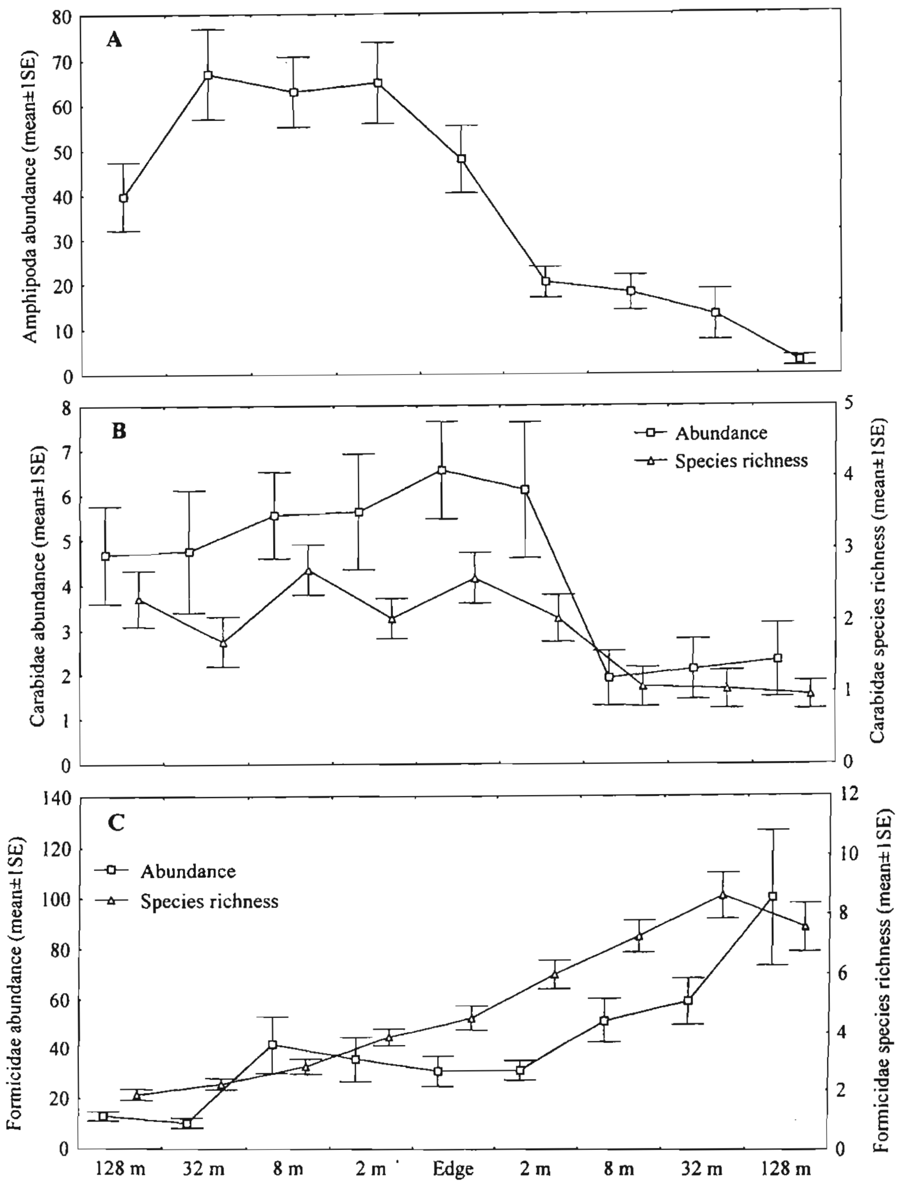


Figure 5. Amphipoda (A), Carabidae (B) and Formicidae (C) mean (±1SE) abundance and species richness across the Afromontane forest patch/grassland matrix ecotone. See text for x-axis explanations.

Everard (1986) showed that unburned *Podocarpus latifolius* Afromontane sites in the KwaZulu-Natal Drakensberg had definite margin-associated vegetation species, and that there was a distinct change in species composition along forest margins as a consequence of fire. Overall, carabid abundance and species richness decreased

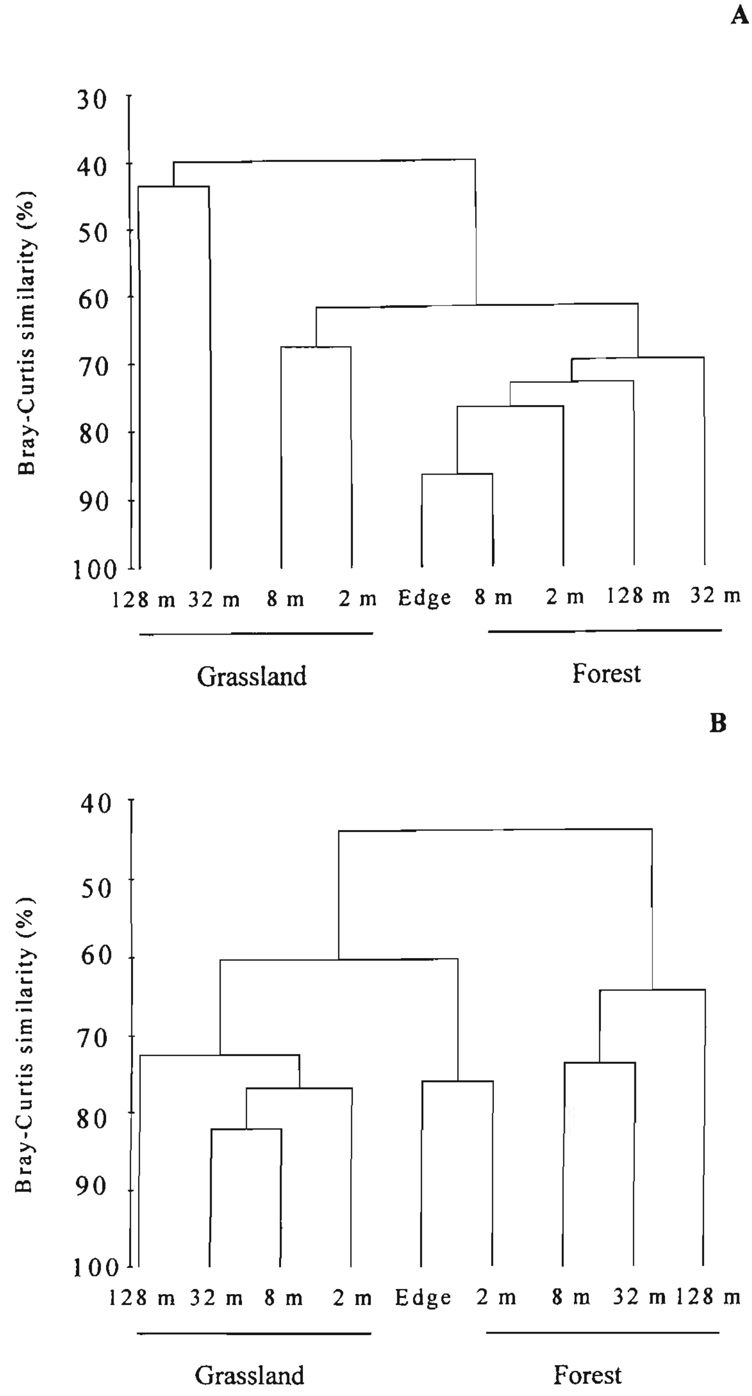


Figure 6. Dendogram for hierarchical clustering of distances across the Afromontane forest/grassland ecotone, based on the Bray-Curtis similarity matrices for Carabidae (A) and Formicidae (B). See text for abbreviation explanations.

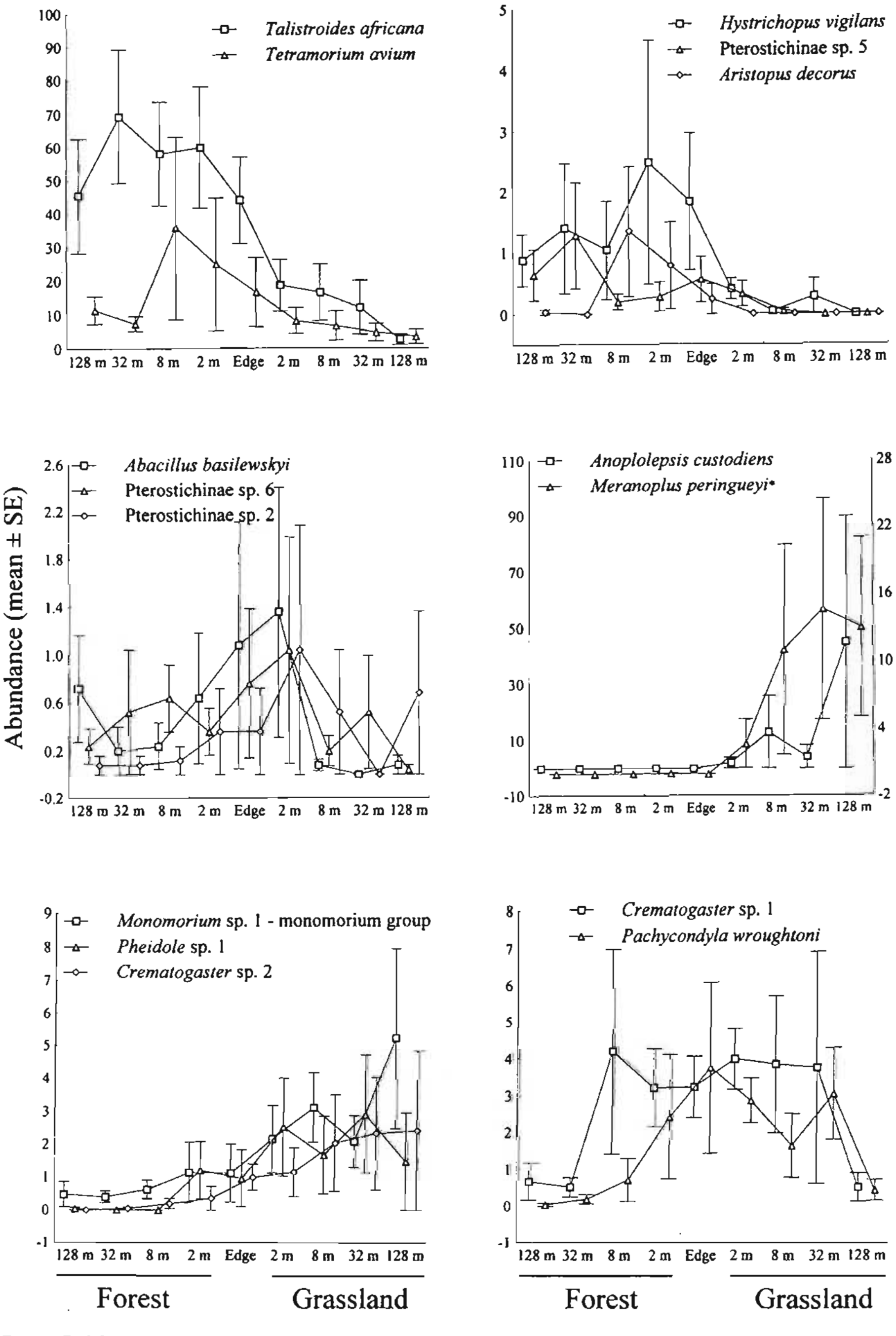


Figure 7. Mean (±1SE) abundances of the most abundant species captured during this study. See text for x-axis explanations. *Meranoplus peringueyi** abundance values on secondary y-axis.

significantly from 8 m onwards into the grassland. At the least disturbed site (Ngeli), however, abundance and species richness were only significantly lower at 128 m into the grassland, while at the most disturbed site (Enon) only a single carabid individual was captured from 8 to 128 m into the grassland. These results covary with disturbance pressures at sites, where Ngeli was the only site with an established transition vegetation (ca. 25 m outside tree line) while Enon showed heavy disturbance in the grassland, with no transition vegetation outside the tree line.

How disturbance in the grasslands influences carabid assemblages in forests is debatable. Anthropogenically-disturbed grasslands perhaps isolate forest patches that are otherwise suitable for carabid colonisation. Also, carabid species have different dispersal abilities, mainly a consequence of wing polymorphism (den Boer 1977; Thiele 1977; Desender 1986), and species with no wings or short wings may find it difficult to cross inhospitable habitat. However, flight ability of the species recorded is not known.

Carabid species turnover (β-diversity) was high at all sites except the least disturbed one (Ngeli). The assessment of turnover is important for determining representativeness (Oliver and Beattie 1996) across these forest/grassland ecotones. These generally high levels of β-diversity across the ecotone indicate a great change in carabid assemblage-composition from forest to grassland.

Changes in ant diversity

Ant assemblages were more similar than carabid assemblages between sites. Overall ant assemblage-structure did, however, differ significantly between sites, but pairwise comparisons between sites showed that ant assemblages between Blinkwater and Karkloof, and Karkloof and Enon did not differ significantly. These sites had similar species lists. Enon (the richest ant site) also shared many species with Ngeli and Blinkwater. The reason why ant assemblage-structure at Enon did, however, differ significantly from that at Ngeli and Blinkwater was the presence of the ant *A. custodiens* at Enon. This aggressive predatory species only occurred at Enon and was the most abundant species captured here (48.9% of total ant abundance at site 5). Samways (1990) showed that *A. custodiens* totally dominated the ant community in a guava orchard, reducing ant richness. Samways (1983) further argued that in newly-created orchards (a highly disturbed habitat) a single ant species can dominate, causing locally low ant diversity. Enon was highly disturbed, particularly the matrix grassland, and although species richness was high here, diversity (incorporating both species richness and abundance) was low. Most interactions between species are antagonistic and selection favours increased competitive ability and predation efficiency (Ricklefs 1987). The exceptionally high abundance of *A. custodiens* at Enon had little effect on ant species richness, but did have an effect on ant abundance. For example, 12 ant species captured at Enon had abundances of less than five individuals, the highest number of rare species at any site. Furthermore, only one carabid individual was captured in the grassland, and only 14 *T. africana* individuals were captured from 2 m inside the forest to 128 m into the grassland. Compared to the other sites, these were very low numbers indeed, and possibly due to the impact of *A. custodiens*.

Ant diversity was also low at Blinkwater, a consequence of the high dominance (Kempton 1979; May 1981) of *T. avium* (72.5% of ant abundance here), and a total of 11 species with less than five individuals captured.

Mean ant species richness did not differ significantly between sites even though only 15 species were captured at Dargle. Significantly higher numbers of ant individuals and species were, however, captured in grasslands, compared to forests. Vegetation connectivity is considerably higher for Afromontane grasslands (Meadows and Linder 1989) than forests, and combined with the observations that; (1) ant richness is high in the grassland; (2) ant species richness did not differ significantly between sites of different disturbance regimes; and (3) ant species may find it easy to colonise areas, a consequence of many ant species producing alate reproductive casts (Hölldobler and Wilson 1990), ant diversity in the Afromontane region is possibly influenced by the distribution of forests and grasslands and biotic interchange through dispersal (Eriksson 1996). Furthermore, high grassland ant diversity suggests that this habitat has been in existence for some considerable time (Ellery and Mentis 1992), and that Afromontane grassland may not just be a simple derivative of past forest presence.

Biotic edge effects

Human impacts are often concentrated near forest edges and greatly exceed natural edge effects in both severity and spatial extent of damage (Matlack 1993). Ecotones between Afromontane forests and grasslands are naturally very sharp, which is possibly a consequence of greater disturbance in the grassland. This seems to be a result of natural grassland, but not forest, fires in the past. However, today the sharpness of these edges is also magnified by anthropogenic fire, vegetation clearing and cattle grazing. Wilson (1982) showed that the spread of *Podocarpus* tree species is inhibited if fire breaks are cleared immediately at the edge of tall forest, leaving no strip for seedlings and saplings to grow. When, however, disturbance intensity is lessened, forest vegetation progresses into grasslands as was observed at Ngeli. Schwartz et al. (1996) showed that forests are advancing into savanna, and although the boundary between forest and savanna is sharp, fire only slows down forest encroachment, but cannot stop it. The ecotone at Ngeli supported vegetation from both adjacent habitat types (i.e. forest and grassland) and had shrubby vegetation unique to the area. None of the other sites supported ecotone vegetation and transition between forest and grassland was characteristically sharp. So too was the overall changes in carabid diversity (abundance and species richness) and assemblage-composition from forest to grassland.

Overall, *T. africana* abundance changed significantly from forest interior to grassland interior, with highest abundance from 32 m inside forests to 2 m inside forests.

The biotic edge effect, defined here as a greater numbers or species at edges compared to interiors (Kroodsma 1982, 1984; Bedford and Usher 1994), was highly evident for *T. africana*. For both amphipods and carabids a clear edge effect was present roughly from the Afromontane ecotone up to 32 m into the forests. Estimation of edge effect penetration, or the distance into a habitat where differences are detected when compared to that habitat's interior (Laurance and Yensen 1991; Chen et al. 1995; Murcia 1995), varies significantly in the literature. Laurance (1991) found detectable ecological changes from 200 up to 500 m into tropical forest fragments, while Chen et al. (1995) showed edge effects from 30 up to 240 m into old-growth Douglas fir forests. Here, at least as indicated by invertebrates, the edge effect was 32 m into the forest. Circular fragments of 5 ha and less will have >50% of its area susceptible to edge effects. Considering that the majority of KwaZulu-Natal Afromontane forest fragments are only between 0.5 and 25 ha in size (Orthophoto survey, Surveyor General, Pietermaritzburg), little interior habitat is available for those species that need such habitat. Also, few patches are circular in shape, and edge effects are especially significant when fragments are irregularly shaped (Laurance and Yensen 1991; Forman 1995).

Where amphipods and carabids showed a significant decrease in abundance and species richness from forest to grassland, ants showed the exact opposite. In fact, carabid and ant species richness covaried negatively ($r = -0.252$, $P = 0.094$), however not significantly, while carabid abundance did not correlate significantly with ant abundance ($r = 0.02$, $P = 0.90$). Nevertheless, higher ant species richness was associated with lower carabid species richness. Carabids share the generalist, surface-active predator guild with at least some spiders and ants, and significant competition can take place between ants and carabids (Thiele 1977; Lövei and Sunderland 1996).

Afromontane forests were poor in epigaeic ants. Also, no detectable edge effect was observed for ants. Dominance of single species, particularly *T. avium* in forests, and *Crematogaster* sp. 1 and *Pachycondyla wroughtoni* at ecotones, were possible agents for low diversity in Afromontane forests. The arboreal component of Afromontane forests was, however, not sampled and Afromontane forests are possibly richer in numbers of ant species than suggested here.

Invertebrate conservation in the KwaZulu-Natal Afromontane region

To conserve carabids in the Afromontane region we suggest that fire and cattle pressure be lessened at ecotones and in the grasslands. The three sites with low disturbance at their interface areas supported similar carabid assemblages and it is probable that carabid propagules exchange between these sites. The two highly disturbed sites probably provide similar forest habitat for carabids, but conditions outside these forests may act as a barrier for beetle dispersal. It is, however, unclear precisely how the ecotone, or the grasslands per se, act as a barrier. Chen et al. (1995) stated that edges play a critical role in controlling ecosystem interactions and landscape function while Dunning et al. (1992) added that an organism's ability to use resources in adjacent patches depended on the nature of the boundary between habitats. The boundaries at Dargle and Enon act possibly as 'obstacles' for propagules attempting to colonise these sites. Alternatively, frequently disturbed edges are more exposed to direct solar radiation, increasing evapotranspiration and are therefore dryer than protected, or older edges (Camargo and Kapos 1995). Less frequent disturbance at Afromontane edges resulted in denser vegetation that 'seals' and protects the forest just inside it (Ranney et al. 1981; Williams-Linera 1990). Webb and Thomas (1993) mentioned that, for invertebrates, the relation between area and species richness is weak, and that edge effects are crucial for species survival and incidence in a particular area. Here, size of forest patch did not explain carabid diversity, but the degree of grassland disturbance, and hence the conditions at the Afromontane ecotone did.

If the conservation options for amphipods and carabids are clear, the same is not true for ants. Although local disturbance did alter ant assemblage-structure at sites selected, no clear 'disturbance-ant diversity' pattern was observed. Nevertheless, grasslands are rich in ant species and should be conserved accordingly. Ant abundance and species richness increased up to 128 m into grasslands with no sign of plateau or decrease, and further research is needed to find out what happens beyond 128 m into both grasslands and forests.

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Appendix. Number of Amphipoda, Carabidae and Formicidae individuals and species captured in this study.

	Ngeli			Blinkwater			Karkloof			Dargle			Enon		
	F	E	G	F	E	G	F	E	G	F	E	G	F	E	G
Amphipoda															
Talistroides africana Griff.	1250	1052	174	731	683	142	795	785	3	495	531	464	630	12	2
Carabidae															
Harpalinae sp. 1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Harpalinae sp. 2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Harpalinae sp. 3	0	0	0	0	0	0	0	0	0	4	3	1	0	0	0
Pterostichinae sp. 2	0	0	0	0	0	0	0	0	0	7	44	30	0	0	0
Pterostichinae sp. 3	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0
Pterostichinae sp. 4	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Pterostichinae sp. 5	36	14	1	7	0	0	10	15	0	0	0	0	0	0	0
Pterostichinae sp. 6	22	43	15	5	3	2	8	8	2	0	0	0	0	0	0
Abacillus basilewskyi Strau.	0	0	0	16	10	3	13	67	1	0	0	0	0	0	0
Aristopus decorus Strau.	1	0	0	28	24	0	1	0	0	3	0	0	1	1	0
Chlaenius sp.	0	4	19	0	0	0	0	0	0	0	0	0	0	0	0
Cophosomorpha angulicollis Strau.	32	17	1	2	1	0	4	0	0	0	0	0	0	0	0
Cophosomorpha caffer Dej.	0	0	0	3	0	8	2	1	22	0	0	0	0	0	0
Craspidophorus graciosus Chaud.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Crytomoscelis ferrugimoides Strau.	2	0	0	2	2	0	0	0	1	0	0	0	0	0	0
Euleptus caffer Boh.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Haplotrachelus sp. 1	13	11	11	0	2	12	0	1	5	0	0	0	0	0	0
Hystrichopus praedator Pèr.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Hystrichopus vigilans Sturui.	13	6	8	60	35	0	10	77	0	0	0	0	0	0	0
Incosa sp. 1	0	0	0	5	9	0	0	0	0	0	0	0	7	2	0
Mesolestinus sp.	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0
Metaxinidium nanum Basil.	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0
Metagonium gilvipes Bot.	0	0	0	0	0	0	0	0	0	4	0	2	0	0	0
Paraxinidium andreaei Chaud.	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0
Systolocranius alternaris Chaud.	2	5	1	0	1	0	1	3	0	3	3	2	0	0	0
Tachyura fausta Pèr.	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Tyronia sp. 1	1	0	0	1	0	0	0	2	0	2	2	0	0	0	0
Xenitenus sp.	0	0	0	0	0	0	0	0	0	6	5	0	0	0	0
Unknown sp. 1	17	21	9	1	1	0	2	0	0	0	0	0	1	0	0
Unknown sp. 2	1	0	0	0	0	0	0	1	0	0	0	0	4	3	0
Number of individuals			330			248			259			127			20
Number of species			15			16			15			12			5

Appendix. Continued.

	Ngeli			Blinkwater			Karkloof			Dargle			Enon		
	F	E	G	F	E	G	F	E	G	F	E	G	F	E	G
Formicidae															
Cerapachyinae															
Cerapachys natalensis Forel	0	0	2	0	0	1	0	0	0	0	0	0	0	0	1
Dorylinae															
Dorylus sp.	0	16	0	0	0	0	1	0	151	0	1	3	30	0	0
Formicinae															
Camponotus congolensis Emery	0	0	0	0	0	0	0	1	1	0	0	0	0	1	13
Camponotus natalensis F Smith, 1858	1	10	50	6	14	23	0	0	0	0	0	0	0	2	0
Camponotus niveosetosus Mayr, 1862	0	1	15	0	6	6	0	6	15	0	0	8	1	2	39
Camponotus sp. – maculatus-group	0	0	1	0	0	0	0	0	8	0	0	0	0	0	2
Lepisiota sp.	0	1	9	0	4	2	0	1	10	0	0	0	0	0	1
Anoplolepsis custodiens F Smith, 1858	0	0	0	0	0	0	0	0	0	0	0	0	0	30	926
Myrmicinae															
Strumigenys sp.	0	0	0	0	0	1	0	1	2	0	0	0	0	0	2
Myrmicaria pallida Arnold, 1925	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Crematogaster sp. 1	20	15	25	1	69	7	8	54	34	31	53	137	45	42	0
Crematogaster sp. 2	0	14	116	1	5	1	0	0	0	5	39	52	0	3	0
Crematogaster sp. 3	0	0	0	0	16	104	0	0	0	0	0	0	0	3	42
Meranoplus peringueyi Emery, 1886	0	13	281	0	0	0	0	0	7	0	0	7	0	33	404
Solenopsis punctaticeps Mayr, 1865	0	1	3	0	0	5	0	5	3	0	0	1	0	0	4
Calyptomyrmex clavisetus Santschi, 1914	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0
Tetramorium avium Bolton, 1980	225	240	26	899	902	26	55	49	254	55	51	31	83	9	23
Tetramorium sp. 1 solidum-group	0	0	13	0	0	1	0	0	0	0	0	0	0	0	0
Tetramorium sp. 2 solidum-group	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11
Tetramorium sp. squaminode-group	0	0	0	0	0	0	0	0	0	2	0	15	0	0	0
Tetramorium sp. sericeiventre-group	0	0	0	0	0	1	0	0	0	0	0	0	0	0	23
Tetramorium sp. 1	6	22	55	0	4	40	1	5	44	0	0	0	1	1	16
Tetramorium sp. 2	0	0	0	0	0	3	0	0	15	0	0	0	0	0	1
Tetramorium sp. 3	0	0	0	0	0	0	0	2	55	0	0	0	0	0	0
Tetramorium sp. 4	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0
Pheidole sp. 1	1	21	111	0	8	1	0	85	12	0	0	1	0	2	16
Pheidole sp. 2	0	0	16	0	21	120	0	0	0	0	0	0	0	0	6
Pheidole sp. 3	0	0	0	0	2	1	0	0	0	0	0	0	0	0	5

Appendix. Continued.

	Ngeli			Blinkwater			Karkloof			Dargle			Enon		
	F	E	G	F	E	G	F	E	G	F	E	G	F	E	G
Monomorium sp. 1 monomorium-group	11	16	52	3	3	32	7	75	39	10	5	32	4	7	63
Monomorium sp. 2 monomorium-group	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0
Monomorium sp. 1	0	0	3	0	6	2	0	0	1	0	0	0	0	0	0
Monomorium sp. 2	0	0	0	0	7	4	0	0	0	0	0	0	0	0	0
Ponerinae															
Streblognathus aethiopicus F Smith, 1858	0	5	23	0	0	0	0	0	0	0	0	0	0	0	0
Pachycondyla wroughtoni Forel, 1901	5	129	63	0	47	7	0	8	36	19	24	1	0	11	13
Pachycondyla peringueyi Emery, 1899	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
Pachycondyla granosa Roger	0	0	6	0	0	27	0	5	28	0	0	0	0	0	1
Pachycondyla sharpi Forel, 1901	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0
Hypoponera transvaalensis Arnold	0	0	0	6	0	0	4	1	2	1	1	0	0	0	0
Leptogenys intermedia Emery, 1902	0	0	0	0	49	15	1	5	0	0	0	0	0	0	0
Leptogenys attenuata F Smith, 1858	3	36	37	0	0	0	0	0	0	0	0	0	1	7	17
Anochetus sp.	0	0	0	0	2	0	0	3	6	0	0	0	0	0	1
Unknown ant species															
Species 1	0	0	217	0	0	0	0	0	1	0	0	0	0	0	0
Species 2	0	0	7	0	0	3	0	0	8	0	0	0	0	0	2
Species 3	0	0	0	4	1	0	1	3	0	0	0	0	1	0	0
Species 4	0	0	0	0	0	0	0	0	1	0	0	0	0	0	6
Species 5	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
Number of individuals			1944			2521			1128			598			1957
Number of species			24			28			27			15			30
Summary															
Number of *T. africana* individuals	7 749														
Number of Carabidae species	30														
Number of Carabidae individuals	984														
Number of Formicidae species	46														
Number of Formicidae individuals	8 148														

Abbreviations: F = forest habitat (128 m into forest to 8 m into forest), E: edge habitat (2 m into forest to 2 m into grassland), and G = grassland habitat (8 m into grassland to 128 m into grassland).

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General discussion with conservation implications

Forman opens his 1995 book, *Land Mosaics*, with the following; 'Animals, plants, water, wind, materials and people move through spatial patterns characteristic of virtually all landscapes and regions'. Moving through a spatially heterogeneous landscape, propagules have to cross, sometimes 'hostile', sometimes 'friendly' matrix habitat, and often architecturally complex habitat edges. These are issues not often dealt with in the scientific literature, but are without a doubt, extremely important in the survival and successful migration of propagules from one suitable habitat to another. Invertebrate dynamics, i.e. dispersal and colonisation success, were not investigated in this study. However, distributions of epigaeic invertebrates in a spatially heterogeneous landscape - the Afromontane forest-grassland mosaic were investigated here. Investigating pattern, and drawing general conclusions from the study, it is possible to identify important structural features in the landscape, features important in terms of invertebrate occurrence and survival.

A cautionary note

Although epigaeic invertebrates are easily and inexpensively collected using pitfall trapping, there are some drawbacks to this method, which have to be taken into consideration when interpreting the results. The main problem in using pitfall traps is that the data it provides may reflect activity density, and not the true densities of the invertebrates it samples (Greenslade, 1964), i.e. the efficiency of the traps is dependent on the activity, or rather, susceptibility of invertebrates to being trapped. In turn, activity of animals is related to weather and their physical environment, and even the hunger level of the animal (Wallin and Ekbom, 1994).

It is, therefore, most likely that all species do not fall into pitfall traps in equal probability. It is also possible that the habitat *per se*, i.e. habitat architecture, and invertebrate size, i.e. larger invertebrates usually move more, affects the probability of capture.

Pitfall traps were used exclusively in this study and the above-mentioned points need to be considered when interpreting the results. For example, most invertebrate collecting took place across a habitat gradient where each end of the gradient was architecturally distinct from the other end. To take two habitat-structure examples; percentage ground cover was significantly less in forests compared to grasslands, while soil compaction was significantly less at the ecotones than in either forest or grassland interiors (chapter II). These physical factors alone will have effects on the movement behaviour of active epigaeic fauna. Consequently, a beetle may move less, or use more energy in architecturally dense grasslands compared to a more open, forest floor.

Pitfall trap design will also influence which part of the community is captured more efficiently, and which part is not (Luff 1987; Holopainen, 1992). Pitfall traps used here were small (mouth diameter = 25 mm), and most likely did not sample the larger species of the taxa selected here. These small traps were, however, used as they are more efficient in capturing smaller species (Luff, 1975; Adis, 1979), which are usually the larger proportion of a community (May, 1981, 1989).

However, future invertebrate collecting in this region, or any other region, should incorporate the use of pitfall traps of different sizes, and whenever possible, the use of other collecting techniques. For example, although more labour intensive, hand collecting and litter-bag sampling should be performed, at least during the initial stages of a study. Results from such a pilot study could be rewarding in terms of how well pitfall trap samples reflect 'real' faunal patterns in the study area, and perhaps will be of use in the selection of more representative fauna to study (i.e. indicator selection, see McGeoch (1998)).

General conclusions

Lack of evidence for an edge effect

Despite Naiman and DéCamps's (1991) claim that ecotones are key landscape elements, the results here show otherwise, with support for the main hypothesis of no evidence for biological or abiotic edge effects across near-natural Afromontane forest-grassland ecotones. Neither carabids nor ants showed a significant elevated mean abundance or species richness at these boundaries. Mean carabid abundance and species richness was high in Afromontane forests, decreased gradually across the sharp forest-grassland boundary, and was low in Afromontane grasslands. An exception to this was in the final study (chapter IV) where carabid abundance and species richness decreased abruptly at the edge into the grassland matrix. Ants on the other hand, were abundant and species rich in all Afromontane grasslands, decreased gradually across all forest-grassland boundaries, and were species poor and rare in all Afromontane forests (chapter II, III, IV).

This hypothesis is in agreement with that of Kapos *et al.* (1997), where they hypothesised that edge effects become less severe, or more complex, as habitat edges mature. In other words, it is not so much the sharpness of edges that plays the dominant role, but the maturity of the transition zone. However, one must bear in mind that this hypothesis was based on observations made from anthropogenically-created habitat edges through time. Afromontane forest-grassland mosaics have existed for, perhaps, millions of years (Lawes, 1990; Eeley *et al.*, 1999) and the hypothesis proposed here concerns natural conditions; edge effects, both biological and abiotic, are not a characteristic of natural, or near-natural habitat junctions.

Certain species did, however, show a preference for edge habitat. For example, *Talistroides africana*, the only terrestrial amphipod species present in the Afromontane region, was consistently, and significantly more abundant at forest-grassland boundaries than in either habitat interiors. It is unlikely that this species is a generalist that has invaded the edge habitat from the surrounding matrix, as suggested by Didham (1997a) for human-disturbed landscapes.

The lack of edge effects in this study clearly holds for carabids and ants at selected Afromontane forest-grassland sites. These groups were selected primarily because of their relative ease of identification in southern Africa, and because of their previous successful use as indicators (see chapter I). They were also selected in agreement with the multi-taxa approach discussed in the first chapter. These focal taxa are probably not representative of all faunas in the Afromontane region. In fact, they are limited to only a tiny fraction of the architecturally complex Afromontane landscape; the epigaeic stratum. The results here could, in future, be supplemented with taxa from phylogenetically distinct groups occupying a diverse number of habitat strata, for example, birds, butterflies, small-mammals and plants.

Faithfulness of assemblage-structure and composition across seasons

An interesting result was that carabids and ants, as individual taxa, showed little inter-seasonal variation in distribution pattern across these ecotones. Although mean summer and spring abundances and species richnesses were higher than those in autumn and winter, and species identities changed from one season to the next, the overall assemblage pattern remained relatively constant. Carabids were almost always more abundant and species rich in the forest compared to the grassland, while ants were always more abundant and species rich in the grassland compared to the forest. This result was unexpected as one might predict intraspecific use of the ecotone to change from one season to the next (Yahner, 1988), thereby making practicality of identifying edge effects difficult.

This is potentially a very exciting result. Insects are sensitive to environmental changes and track climatic alterations (Wolda, 1983; Strong *et al.*, 1984; Niemelä *et al.*, 1989, 1994; Samways, 1994). This is true for individual species, but perhaps not necessarily so for assemblages as a whole, in tropical and subtropical areas. This hypothesis could be further tested in other subtropical areas, and particularly in the tropics where one might expect even less variation, in terms of invertebrate pattern, between seasons.

Grassland matrix effects on the forest patches

The Afromontane landscape consists of a network of natural forest patches scattered in a grassland matrix of variable quality. Most human activities take place in these grasslands, with concurrent loss of ecological integrity. The results here show that the grassland matrix has a significant influence on the organisms at forest-grassland boundaries and in the forest patches (Saunders *et al.*, 1991). Matrix characteristics are important because they determine the survival rate of individuals moving between remnant patches of habitat (Fahrig, 1999). In fact, the lower the matrix quality, the more resistant is a landscape to flow of species, energy and materials through it (Forman, 1995).

Metapopulation theory can benefit substantially from studies on matrix characteristics (Saunders *et al.*, 1991; Fahrig 1999), or landscape resistance (Forman, 1995). In short, the metapopulation concept hypothesises that populations are spatially structured into assemblages of local breeding populations and that migration among the local populations has some effect on the local dynamics, including the possibility of population reestablishment following extinction (Hanski and Simberloff, 1997). Space is, therefore, an important component in any species' life, and how individuals of a species perceive, or react to spatial components in the landscape, will ultimately determine the well being of the species in the landscape. Of course, not all patchy systems should automatically be viewed as a metapopulation system, but for those that follow metapopulation criteria, an understanding of the influences of the surrounding landscape, i.e. the matrix and habitat edges on movement and survival of migrating propagues, may vastly improve models that are closely linked with empirical field studies, i.e. spatially realistic models (Hanski and Simberloff, 1997).

Ecological implications of findings for invertebrate conservation

Apart from their immense diversity, invertebrates are especially important in wildlife conservation due to their sensitivity to environmental changes (Dempster, 1991). Although abiotic factors such as climate and weather, i.e. density-independent factors, influence invertebrate numbers, anthropogenic modification of the landscape has become a principal factor in altering invertebrate community structure (Samways, 1994). The world's biota is systematically being homogenised through human activities like urbanisation, agriculture and the introduction of exotic species (Elton, 1958; Spence and Spence, 1988; Samways, 1999). At the landscape level, however, heterogeneity increases principally through anthropogenic fragmentation (Forman, 1995). What were formerly large tracks of native vegetation are being dissected, fragmented and isolated through human activities like agriculture, settlement and afforestation (Hunter, 1996).

In heavily fragmented landscapes, edges become a major, even dominant visual feature (Laurance, 1997). Therefore, as landscape heterogeneity increases, so does the amount of habitat edge. These anthropogenically-created edges can provide opportunities for invasion of the remnant patches by weedy or generalist plants and animals (Laurance, 1997). In fact, invertebrate abundance and species richness is known to increase towards artificial edges, in particular forest edges, and it is argued that this increase is probably due to the replacement of the natural forest community with invasive, generalist species (Halme and Niemelä, 1993;

Usher *et al.*, 1993; Didham 1997a, b). If fragmentation of the landscape continues at its current rate, the end-result would most probably be an impoverished, homogenised globe, where simple ecological systems are anthropogenically controlled and maintained for the production of food (i.e. simple pollination systems in agricultural ecosystems).

There exists a genuine need for studies on the effects of forest fragmentation on invertebrates (Klein, 1989; Didham, 1997b). Of particular interest are the effects of habitat edges (Murcia, 1995; Risser, 1995) and the quality of the surrounding matrix (Forman, 1995; Fahrig, 1999) on invertebrate survival and dynamics in habitat patches.

The Afromontane region provides excellent, and many new opportunities for ecological research. For example, according to the categorisation by Adejuwon and Adesina (1992) (see general introduction), ecotones in the Afromontane region fall into category one, where two contrasting communities compete for space at their point of junction. These edges produce no intermediates, and the edge of either community is continually advancing or retreating. According to Forman and Godron (1981) these abrupt ecotones are usually a consequence of increased disturbance in the landscape, or, according to Báckeus (1993) when the main environmental factor is present on only one side of the boundary. Here, in the Afromontane region, fire occurs frequently in the grasslands and is mainly responsible for this sharp transition between forest and grassland. However, these visually-sharp ecotones were not reflected in the distribution patterns of the epigaeic invertebrates captured. It appears, then, that these invertebrates do not perceive the landscape the same way we do, and react almost as if the boundary *per se* was relatively irrelevant (more on this in the Afromontane edges section below). And although certain abundant species showed definite affinities to either forest (e.g. Pterostichinae sp. 2) or grassland (e.g. *Meranoplus peringueyi*) habitat, no species (with the possible exception of *Crematogaster* sp. 2, F:E:G ratio = 20:3:77, chapter III) actually avoided the edge.

Moreover, the Afromontane flora probably has had a more complex origin and evolutionary history than any other in the world (White, 1981; Matthews *et al.*, 1993). Unfortunately, the Afromontane system is among the most threatened in southern Africa (Macdonald *et al.*, 1993). This system, and in particular Afromontane grasslands, are under considerable pressure from commercial forestry, invasion by alien plants (Matthews *et al.*, 1993; Allen *et al.*, 1997) and cattle overgrazing (Tainton, 1981; Hockey *et al.*, 1988).

Afromontane forests

Although approximately half of the 40 141 ha of Afromontane forests are protected (Geldenhuys and MacDevette, 1989), these are isolated from one another by zones of grassland and, mainly, anthropogenically-altered habitat. The rest of the Afromontane forests are situated on private- or forestry-owned land, and although land-owners see natural forests on their land as an asset, conservation guidelines are, as yet, not readily available to assist in conserving these natural resources.

The study here showed that Afromontane forests are rich in carabid species and high in carabid individuals. However, with smaller forest patch-size and increased disturbance at the forest boundary, carabids decreased in species richness and abundance. Small forest patches (< 25 ha) were depauperate in a number of carabid species. The large forest patch at Enon, with exceptionally high anthropogenic disturbance in the surrounding grassland, was also relatively low in carabid species. The majority of KwaZulu-Natal Afromontane forest fragments are smaller than 25 ha (Orthophoto survey, Surveyor General, Pietermaritzburg), and it could be argued that these patches are not worth conserving. These very small forest patches however, form part of an extensive Afromontane forest patch network partly making up the 'forest belt', east of the Drakensberg mountains (Cooper, 1985; Eeley *et al.*, 1999). They appear important in aiding species in travelling from one suitable habitat patch to the next, or in the metapopulation dynamics of certain species (Wiens, 1996; Hanski and Simberloff, 1997). For example, *Talistroides africana* was abundantly captured in both small and large forest patches, and was not strongly influenced by patch size.

Afromontane grasslands

The main vegetation type in the Afromontane region is '*Themeda triandra* dominated grasslands' (Acocks, 1988), and is considered by some as a secondary fire-maintained vegetation type (White, 1983; McCracken, 1986). However, this is contradicted by the fact that nearly all floristic endemics in the region are grassland species (Matthews *et al.*, 1993; Jansen *et al.*, 1999). Although rich in floristic endemics, only 2% of this grassland biome in South Africa is protected (Siegfried, 1992).

The results here showed that native Afromontane grasslands are consistently significantly richer in ants than Afromontane forests. Ant assemblage-structure in these grasslands was also significantly different from that of forests. It is, however, still unknown how grassland alterations influence invertebrate communities.

There was not a significant decrease in ant species richness with increased disturbance, but there was a significant change in ant assemblage-structure with an increase in disturbance. *Anoplolepsis custodiens*, a native and dominating ant species (Samways, 1997), was absent from most grasslands studied, but was present, and most abundant, in a highly disturbed grassland at Enon (chapter IV). This species is an aggressive predator and was perhaps responsible for the almost complete absence of carabids and amphipods in this grassland. Clearly, such levels of grassland disturbance should be avoided, since the appearance of such a competitively superior, albeit, native species, will influence local and regional diversity patterns in the Afromontane region.

Furthermore, there has been a recent recognition of the importance of the quality of the surrounding matrix in the survival probability of organisms moving between suitable habitat patches (Wiens, 1996; Fahrig, 1999). The matrix may not simply be a sink for species moving between suitable habitat, but unlike oceanic islands, may provide some resources and cover for dispersing individuals. Native, relatively undisturbed Afromontane grasslands may facilitate in the dispersal of individuals from one forest patch to the other. This was illustrated in chapter IV where carabids and amphipods were present in relatively undisturbed grassland sites, but virtually absent from the most disturbed site (Enon). However, since only a single highly disturbed site was available for study, this could not be confirmed. A genuine need exists to study the effects of matrix quality (here Afromontane grassland quality) on the survival probabilities of organisms moving between suitable forest habitat. By reducing cattle pressure and fire frequency, matrix quality is likely to improve, and so too will the survival probability of organisms in both grasslands and forests. Fire should, however, not be completely excluded, as it is a natural process in the region. Also, Morgan and Lunt (1999) showed that inter-fire intervals of more than one year and less than five years is a necessity in *Themeda triandra* dominated grasslands in Australia, in order to maintain the health and vigour of this dominant grass, and also to maintain a high native plant diversity. Without data from the Afromontane region it is difficult to apply these results from Australia to the South African system. Research on this is urgently needed.

Afromontane edges

In many instances, edge effects caused by humans can be the principal cause of population declines (Laurance, 1997). Furthermore, it has been suggested that the leading role in landscape ecology is played by edges (Jagomägi *et al.*, 1988). This is, perhaps, true in heavily disturbed landscapes, but in more natural ones, as is the case here, it appears that edges have little effect on the resident fauna. This is the case even though Afromontane forest-grassland ecotones are sharp and the result of a mostly natural disturbance, particularly fire, rather than artificial and severe disturbances, like clear-cutting and agriculture. Modifications in environmental conditions at newly-created edges disappear, or become more complex, as edges mature (Kapos *et al.*, 1997), and this is also true for Afromontane forest-grassland boundaries. Most environmental variables selected changed only gradually across Afromontane forest-grassland ecotones, as did carabid and ant abundance and species richness.

A number of species did, however, increase in abundance at the boundary, and true edge species could be identified, because sampling took place across seasons (see Yahner, 1988). *Talistroides africana* was notable in this regard. The significantly higher abundance of *T. africana* at the ecotone implies high decomposing activities here

(Friend and Richardson, 1986; Margules *et al.*, 1994). This coincided with lower soil compaction at the ecotone compared to that at the habitat interiors (chapter III). Also, the fire-resistant tree species *Leucosidea sericea* dominated edge vegetation. Almost all litter found at the edges was from this tree species (pers. obs.) and was a highly suitable habitat for this amphipod. The importance of this is mentioned in the future research section.

Edge effects consist of three components, direct biological, indirect biological and abiotic (Murcia, 1995). The emphasis of this thesis was mainly directed towards direct biological and abiotic edge effects, but it is important to recognise the importance of indirect biological edge effects. Dispersing individuals, after crossing a matrix, encounter edges that can be hostile in a number of ways (Wiens, 1996). Firstly, habitat edges are often architecturally more complex than habitat interiors (Lovejoy *et al.*, 1986), and propagules may consequently spend more time at the edge, due to difficulty in moving to more suitable interior habitat. Secondly, predation and parasitism are known to be high at edges (e.g. Noss, 1987; Andrén and Angelstam, 1988), which decreases the survival probability of individuals moving through them. Indeed, Ingham and Samways (1996) showed that scorpions are more abundant at the edge than in either Afromontane forest or grassland interiors. Apart from potentially higher predation rates at edges, species interactions probably also change from one season to the next. The results here showed that few carabid and ant individuals were captured at the Afromontane forest-grassland edge during winter and autumn, while amphipod abundance was relatively high at the edge during these seasons (chapter III). Amphipods perhaps escape much predation from carabids and ants during autumn and winter.

To conclude, edge effects, both biological and abiotic, are either absent or very complex at Afromontane forest-grassland boundaries. Although both carabids and ants showed no direct biological edge effect, certain species did increase significantly in abundance at these boundaries. Certain abiotic factors changed significantly across the ecotone, but most changed gradually from forest to grassland. Finally, carabid and ant distribution patterns across these ecotones changed little from one season to the next. Nevertheless, species interactions probably change inter-seasonally, because species identities changed from one season to the next.

The following conservation implications and suggestions flow from this study. A number of proposals for future research are made based on results obtained from this thesis.

Conservation recommendations

- It is imperative to investigate more than one taxon in conservation research (di Castri *et al.*, 1992), as different taxa often show markedly different responses to a given environmental condition. In this study, little covariation was found among invertebrate taxa in terms of species richness. It is recommended that at least two taxonomic groups are used, and if resources and taxonomic expertise were available, more would be better still. Carabids and ants have been used extensively, but independently, in many invertebrate ecological studies (Niemelä, 1996; Andersen, 1997; Niemelä *et al.*, 2000), but as was shown here, when studied together can improve, or change conservation implications considerably. It is important to realise that different taxa will differ in their responses to fragmentation or other ecological phenomena (Niemelä and Baur, 1999), so it is furthermore recommended to include other groups as well, such as birds, small mammals, butterflies and plants. The emphasis of this result, however, is on the application of this knowledge to conservation decisions.

- The protection of native Afromontane grasslands should be top priority in South Africa. Human disturbances like settlement, forestry, cattle farming and agriculture are concentrated in Afromontane grasslands. Also, fire is an almost annual event in the region and is mainly responsible for the sharp transition between forest and grassland. These disturbances severely influenced amphipod, carabid and ant distribution and diversity patterns in the Afromontane region. The protection of native grasslands through not-too-frequent burns (see below) and sustainable grazing levels is recommended, and in particular, their protection at forest boundaries. In this way, not only will some indigenous grassland be conserved, but also the interface between forest and grassland, and consequently Afromontane forests.
- Ant species richness increased up to 128 m into grasslands with no sign of plateau or decrease. I recommend the protection of Afromontane grasslands at least up to 150 m from forest edges. In this way, the unique ant assemblage found in Afromontane grasslands will be protected. This is, however, only a start, and future conservation priorities should be directed towards protecting the endemic-rich grassland *per se*, as only 2% of this habitat type is currently under protection.
- In the past, Afromontane forests have undergone severe human exploitation (see Lawes and Eeley, 2000). At present however, many of the larger tracks of forests are protected, while smaller forest patches are scattered throughout the Afromontane region, mainly situated on private or forestry-company land. Many private owners consider native forests an asset, but they nevertheless burn grasslands surrounding these forests. Fires do not normally penetrate forests and are, therefore, allowed to burn-out at forest edges. However, with an almost annual fire regime in the Afromontane region, forest succession into grasslands is prevented and in some instances, fires do penetrate forests. It is recommended that fires should be less frequent (e.g. every four to five years), and directed away from

forest boundaries to protect edge habitat. This would protect forests and promote forest expansion. Fire is a natural occurrence in the Afromontane region and, in fact, the burning of *Themeda triandra* (the dominant grass species here) at least every five years is necessary to maintain the health and vigour of this species (Morgan and Lunt, 1999). Nevertheless, frequent fires coupled with intensive cattle grazing will undoubtedly continue to change the character of Afromontane grasslands, potentially influencing, and changing, the whole Afromontane region dramatically. Unfortunately, this recommendation is in conflict with cattle farming practices. Farmers prefer to burn grasslands on an annual basis, before the rainy season, to provide new growth for their cattle. This would be an important discussion point for the local conservancies.

Future research

As little ecological work has been conducted on invertebrates in the Afromontane region and the following are some future research suggestions:

- There was no evidence to support the biological, or abiotic, edge effect hypothesis at natural Afromontane forest-grassland boundaries, suggesting that edge effects are perhaps more characteristic of human-disturbed landscapes, rather than natural ones. This hypothesis, however, needs further rigorous testing on taxa besides carabids and ants. These two groups are not as directly dependent on vegetation as some hemipteran groups. Lygaeidae, a seed-predator family in the order Hemiptera, was captured in abundance using pitfall traps (see general Appendix), and could be investigated further. Vegetation is often denser at habitat edges, and organisms directly dependent on vegetative matter may show different distributional patterns than those that are not directly dependent. Lygaeids, being seed-predators, may also be important in terms of forest-structure characteristics and forest-grassland distributional dynamics. Future research could include, testing other taxa at these natural boundaries, and testing the edge effect hypothesis at other natural habitat boundaries.
- Although naturally sharp, Afromontane forest-grassland edges are, perhaps, even sharper today as a result of an almost annual burning regime in the grasslands. Observations at Ngeli (one of the least disturbed sites selected here, chapter IV) suggest that with the exclusion of fire, unique transitional vegetation does develop between forest and grassland. The transition between forest and grassland at Ngeli was still sharp (about 25 m), but less so than at other, frequently-burned sites. Detailed studies are required on the effects of fire on the regional distribution, occurrence, and expansion/contraction of Afromontane forests. Specific questions

include: Will the exclusion of fire lead to forest expansion? Will the exclusion of fire lead to the development of unique edge vegetation, and consequently a unique faunal assemblage at these ecotones? If fire is excluded from the Afromontane region for some time, will the accumulation of vegetative matter in the grasslands and at the edges be a fire hazard? These are important questions that need urgent attention in the Afromontane system.

- Studying the effects of afforestation on invertebrate communities is important. Forestry is a major industry in the Afromontane region and large tracks of native grasslands have been, and still are, converted to plantations of exotic trees. The results here showed that Afromontane grasslands are rich in ant species and converting grasslands to exotic plantations may have a severe local effect on ant, and other invertebrate assemblages. Comparing grassland and plantation fauna, and even testing the edge effect hypothesis at these human-induced edges will further our knowledge on the effects of humans in the Afromontane landscape.
- Agro-forestry (particularly pine plantations) can isolate populations of certain taxa. This means that certain organisms are relatively isolated, with dispersal to and from other natural forest patches adversely affected. This is because most agro-forestry transforms Afromontane grasslands thereby reducing the quality of the grassland matrix. Research on the metapopulation structure of forest species, e.g. certain carabids, may reveal whether these forest patches are in fact isolated in terms of invertebrate forest species, and how invertebrate communities are affected by this isolation. Research in the Afromontane region provides an excellent opportunity to test metapopulation theory, as was shown by Saccheri *et al.* (1998) for butterflies on the Åland islands, Finland.
- *Talistroides africana*, the only amphipod species captured here, needs further investigation. This species was the most abundant species captured using pitfall traps and is abundant in Afromontane forests and at the edge. *T. africana* is a litter decomposer and appears to provide a valuable function in the ecosystem. Exclusion experiments, by means of fine-mesh litter bags, can provide valuable information on this species' role in Afromontane forest systems, and in particular in forest establishment and expansion. *Leucosidea sericea*, a fire-resistant tree species commonly found at forest edges (Acocks, 1988), also occurs as singletons in Afromontane grasslands. This scattered distribution in grasslands may denote earlier presence of Afromontane forest patches, or alternatively this species may be a precursor for forest establishment. *L. sericea* produces high volumes of leaf litter, a suitable habitat for *T. africana*. Long-term research on the presence, and function, of *T. africana* in these *L. sericea*-dominated patches can

shed light on the dynamics of the Afromontane region. Specific questions include: Does *T. africana* occur at high abundance in small stands of *L. sericea*? Is there a critical size at which forest interior tree species enter *L. sericea* stands? And, what is the functional role of *T. africana*, if any, in Afromontane forest establishment and/or expansion?

- At many of the sites selected, there was extreme dominance by certain individual species. For carabids, Pterostichinae sp. 2 was extremely abundant in the Impendle district, in Dargle (chapters I, II, III, and the Dargle site in chapter IV), while *Hystrichopus vigilans* was the most abundant carabid regionally (chapter IV). For ants, *Crematogaster* sp. 1 was dominant in the Dargle area, while *Tetramorium avium* was so regionally (chapter IV). Of course, certain species are more abundant than others, but the interesting point here was that Pterostichinae sp. 2 was extremely abundant in Dargle, but did not occur at all at any of the other sites (chapter IV). This species may be an endemic, or an aggressive invader to disturbed sites, and future research is required to evaluate this. Also, the effects of the predacious and abundant ant species *Crematogaster* sp. 1, as well as the seed predator and abundant ant species, *Tetramorium avium*, on the Afromontane system, need further investigation.
- A number of other epigaeic invertebrate groups occurred in abundance in the pitfall traps, and need further investigation in terms of their function and distribution in the Afromontane region. These include spiders (Araneae), springtails (in particular the springtail family Entomobryidae), rove beetles (Staphylinidae), cryptophagids (Cryptophagidae) and weevils (Curculionidae).
- Finally, the ecotonal distribution and diversity patterns of amphipods, carabids and ants remained more or less the same, but at different abundance levels throughout the year. These Afromontane sites however, lie in a part of the world highly susceptible to the vagaries of the El Niño southern oscillation. It would be particularly interesting to investigate whether these patterns remain in severe drought or heavy rainfall years. In such years, do these small patches lose and/or gain species? In other words, are these patterns static or highly dynamic?

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General appendix on non-focal taxa captured in this study

Data on many invertebrates captured in the present study were not statistically analysed. These specimens (or by-catch) were, nevertheless, identified into major taxonomic units, and for some, to species level. Pitfall traps do not adequately sample invertebrates other than epigaeic ones. Even so, this trapping technique samples active epigaeic invertebrates more efficiently than passive ones. In this appendix we present the by-catch invertebrates obtained during the study period (except for the chapter IV samples).

Many invertebrate taxa are not epigaeic, notably Diptera, Lepidoptera, Hymenoptera (excluding Formicidae), and groups within orders Hemiptera and Coleoptera.

Furthermore, certain groups contain large species which could not have been sampled adequately with the techniques used, for example Diplopoda, Arachnida, Orthoptera and others. This by-catch appendix is included to provide baseline information on some of the other invertebrate groups present in the Afromontane region, and which may be useful to future studies.

Site location: Farm Nhlosane, Impendle (29°35'S 29°58'E), KwaZulu-Natal, South Africa (chapter I, Fig. 1).

Date of sampling: October 1993 to November 1994.

Appendix. Total invertebrate by-catch (presented as total abundance per taxon) over the 14-month study period, from October 1993 to November 1994 (values represent total abundances per species, or group).

	1993*			1994										
Invertebrate name	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov
Crustacea														
Isopoda	402	986	419	225	215	227	164	58	61	68	42	80	181	169
Chilopoda														
Cormocephalus sp.	0	1	2	0	0	0	0	0	0	0	0	0	0	0
Paralamycetes spenceri	53	82	48	41	26	30	22	22	15	8	6	8	22	19
Lamycetes sp.	96	229	75	84	113	98	123	44	22	10	7	8	34	38
Unidentified sp.	1	2	1	2	0	0	0	1	0	0	0	0	0	0
juvenile	0	34	19	7	16	56	16	3	5	3	6	17	20	17
Diplopoda														
Spirostreptidae	7	35	25	6	3	10	1	0	0	0	0	1	6	21
Odontopygidae	19	36	4	1	2	0	0	0	0	0	0	0	9	10
juvenile	0	2	1	3	1	0	0	0	0	0	0	0	0	0
Pachybolidae juvenile	146	60	36	15	17	7	1	0	0	1	0	4	47	33
Polydesmida	379	612	192	159	115	185	298	62	22	24	21	33	99	201
Sphaerotherium spp.	249	172	29	42	29	46	57	18	0	0	0	5	42	70
Unidentified sp.	0	0	3	5	2	3	0	0	0	0	0	2	2	1

Appendix *(Continued)*

	1993*			1994										
Invertebrate name	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov
Arachnida														
Acari: Acarina (mites)	535	1232	291	60	23	30	170	182	193	68	35	129	245	227
Acari: Ixodida (ticks)	51	110	116	113	61	67	15	4	13	4	1	1	22	17
Opilionida														
Triaenonychidae	51	19	14	4	0	4	15	9	4	1	4	2	14	16
Phalangiidae	209	145	19	29	18	5	18	25	52	50	55	138	128	44
Unidentified spp.	26	56	2	1	0	0	2	0	2	2	1	31	22	14
Scorpionida	0	0	1	0	0	1	0	0	0	0	0	0	0	0
Pseudoscorpionida	1	6	5	5	1	6	4	1	0	0	0	2	1	2
Araneae														
Aglenida	0	0	1	1	0	0	0	0	0	0	0	0	0	0
Amaurobiidae	25	10	5	8	6	10	48	5	1	1	7	0	1	2
Araneidae	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Clubionidae	0	3	12	8	3	4	8	1	3	1	0	0	4	6
Gnaphosidae	30	33	13	3	2	31	43	25	15	5	4	1	5	36
Hahniidae	76	52	31	8	15	21	22	15	30	14	16	22	32	51
Linyphidae	0	34	53	18	9	3	45	52	6	0	0	1	56	102
Lycosidae	2	1	1	1	1	3	8	2	28	15	20	9	2	1
Miturgidae	24	23	12	5	5	6	17	4	9	10	7	10	6	7
Nemesiidae	54	97	25	6	2	3	10	2	0	0	0	4	18	43
Oonopidae	4	26	1	0	0	0	0	1	0	10	1	4	2	3
Palpimanidae	0	1	0	0	0	0	1	0	0	0	0	0	0	0
Salticidae	32	73	41	19	15	15	13	3	9	6	0	7	24	27
Scytodidae	12	21	4	5	0	4	2	4	16	6	2	3	13	10
Tetragnathidae	23	24	3	4	1	4	17	3	5	7	5	16	54	71
Theriidae	0	1	0	0	0	0	0	0	0	0	0	0	0	2
Thomisidae	0	4	0	4	0	0	3	2	0	2	1	0	0	0
Zodariidae	71	165	78	49	114	289	364	127	139	100	45	43	72	67
juvenile	17	12	7	20	5	8	24	10	11	7	9	7	14	9
Unidentified spp.	197	643	114	73	73	60	66	53	53	14	25	56	147	204
Collembola														
Entomobryidae	733	2647	814	912	686	912	1615	1638	1331	880	374	1948	1862	1049
Onychiuridae	0	8	20	21	4	23	35	8	2	0	0	0	4	0
Isotomidae	0	10	7	3	4	19	8	13	5	9	4	7	9	19
Sminthuridae	0	89	95	30	29	41	39	13	7	0	0	26	3	21
Archaeognatha	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Blattodea	28	42	6	8	8	11	10	5	5	10	0	7	15	29
Mantodea	0	2	0	0	0	0	0	0	2	4	0	0	0	0
Dermaptera	23	115	27	17	10	17	36	49	34	25	15	32	63	56
Orthoptera														
Gryllacrididae	33	141	38	14	17	33	21	4	0	2	0	2	29	19
Tetigoniidae	4	15	0	1	1	0	0	2	0	0	0	0	0	0
Gryllidae	25	114	23	80	153	243	54	2	0	0	0	2	5	14
Ensifera	19	53	100	73	22	8	1	1	2	4	2	2	6	2
Acrididae	3	21	0	0	1	2	2	3	13	13	0	4	0	0

Appendix *(Continued)*

	1993*			1994										
Invertebrate name	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov
Tetrigidae	5	25	4	5	0	0	0	0	2	0	0	0	1	1
Psocoptera														
Psocidae	0	13	0	0	0	0	2	0	1	1	0	0	0	0
Caeciliidae	1	14	0	0	0	2	2	0	0	1	0	2	0	0
Ectopsocidae	0	1	1	0	0	0	0	1	0	0	0	0	0	1
brachypterous Psocoptera	1	1	0	6	1	0	1	1	0	0	0	0	0	1
nymph	0	8	1	3	0	1	2	2	4	1	0	1	0	0
Unidentified female	0	0	0	0	0	2	2	0	0	0	0	1	0	1
Hemiptera														
Heteroptera														
Dipsocoridae	0	1	8	3	4	1	1	0	0	0	0	0	3	4
Cimicidae	31	29	16	2	2	1	5	11	10	1	1	4	22	20
Nabidae	14	13	5	2	0	0	0	2	0	0	0	0	3	4
Reduviidae	1	0	1	0	0	0	0	0	0	1	2	0	0	0
Aradidae	0	4	2	0	0	0	0	0	0	0	0	0	2	0
Lygaeidae	321	1320	914	891	558	396	358	125	50	25	93	245	362	312
Cydnidae	23	62	9	8	19	8	8	3	4	1	1	4	7	10
nymph	86	108	28	19	11	8	8	17	14	6	13	34	58	33
Homoptera														
Delphacidae	0	0	0	0	3	0	0	0	0	0	0	0	0	0
Aphrophoridae	1	4	5	10	3	0	1	0	1	0	0	0	2	0
Cicadellidae	13	66	22	21	6	16	16	17	12	25	15	16	21	16
Aphididae	25	133	43	26	47	51	25	13	15	7	6	6	5	13
Pseudococcidae	0	0	1	0	0	0	0	1	1	0	0	0	0	0
nymph	0	2	22	56	6	4	1	0	0	0	1	1	3	1
Diptera														
Nematocera														
Tipulidae	56	90	24	12	8	10	17	44	3	4	3	3	12	13
Psychodidae	0	0	0	0	0	0	5	3	1	0	0	0	0	1
Chironomidae	86	426	67	71	61	23	16	4	9	9	1	9	16	26
Simuliidae	0	1	0	0	0	0	0	0	0	0	0	0	1	0
Bibionidae	0	1	3	0	1	2	0	1	2	0	0	1	2	0
Mycetophilidae	7	11	195	32	10	29	9	0	0	1	0	20	15	2
Sciaridae	377	641	95	50	72	38	46	48	64	34	15	124	534	104
Cecidomyiidae	0	0	0	0	1	0	0	0	0	0	0	0	1	7
Brachycera														
Stratiomyidae	0	1	0	16	15	1	0	1	0	0	0	0	0	0
Tabanidae	0	2	0	0	0	0	2	0	0	0	0	0	0	0
Rhagionidae	3	5	0	0	0	0	0	17	0	0	0	0	2	1
Asilidae	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Empididae	0	21	33	18	16	8	27	32	21	7	0	3	13	20
Dolichopodidae	0	0	2	6	4	4	1	1	0	0	0	0	0	1
Cyclorrhapha														
Phoridae	152	723	252	253	214	141	93	126	69	27	34	170	322	116
Syrphidae	0	0	0	0	0	0	0	1	1	0	0	0	0	0

Appendix *(Continued)*

	1993*			1994										
Invertebrate name	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov
Tephritidae	0	0	2	0	0	0	0	0	0	0	9	1	0	0
Platystomatidae	0	0	5	6	0	2	0	0	0	0	0	0	0	0
Diopsidae	7	26	7	9	2	0	0	2	5	1	0	6	2	6
Sepsidae	2	18	3	5	0	0	0	0	1	0	2	3	16	6
Chamaemyiidae	0	6	1	3	0	0	0	0	0	0	0	0	0	0
Lauxaniidae	5	3	1	3	0	0	0	0	3	3	0	1	2	1
Heleomyzidae	63	129	37	79	72	90	223	375	240	185	17	61	67	84
Sphaeroceridae	257	630	247	338	287	330	112	84	115	95	55	174	156	211
Ephydridae	0	6	0	0	0	0	1	0	0	0	4	0	0	0
Drosophilidae	102	2297	1719	204	298	370	58	19	40	21	18	11	56	125
Milichiidae	7	18	7	1	2	1	1	1	2	0	0	0	3	1
Chloropidae	0	0	2	0	0	2	0	0	2	1	1	6	5	0
Scathophagidae	0	2	0	1	0	0	0	0	0	0	0	0	0	0
Muscidae	18	92	46	104	77	64	255	420	1095	167	14	32	70	35
Calliphoridae	3	64	0	2	4	2	0	0	0	0	0	0	15	19
Sarcophagidae	0	6	0	0	0	1	1	0	0	0	0	0	0	1
Tachinidae	0	3	1	7	1	2	7	6	0	0	0	0	4	5
Diptera larva	52	57	11	8	6	88	19	4	0	0	0	0	6	10
Neuroptera	0	3	0	0	0	0	1	3	2	4	2	7	24	1
Coleoptera														
Adephaga:														
Caraboidea														
Cicindelidae	0	2	2	1	0	0	0	0	0	0	0	0	0	0
Polyphaga:														
Hydrophiloidea														
Hydrophilidae	28	42	19	15	3	11	4	3	0	0	0	0	3	4
Histeroidea														
Histeridae	1	20	13	0	10	6	0	0	0	0	0	0	0	16
Staphylinoidea														
Ptillidae	0	19	8	3	7	6	2	4	2	24	47	41	69	68
Leiodidae	0	69	142	150	57	33	32	28	12	3	26	34	31	27
Scydmaenidae	6	32	4	5	2	3	25	57	63	64	28	30	21	10
Scaphidiidae	1	5	10	8	4	4	5	0	12	7	0	0	0	0
Staphylinidae	1430	3596	1536	1468	1417	1128	703	273	165	70	162	414	722	881
Pselaphidae	8	3	2	1	7	6	10	4	4	2	2	4	6	7
Scarabaeoidea														
Trogidae	37	91	6	1	4	0	4	1	0	1	2	5	8	5
Scarabaeidae	81	111	39	24	11	11	8	3	1	1	0	1	7	9
Byrrhoidea														
Byrrhidae	4	39	5	7	5	1	3	2	2	4	7	26	35	19
Elateroidea														
Elateridae	0	0	4	3	0	0	0	0	0	0	0	0	0	0
Cantharoidea														
Cantharidae	0	0	2	0	0	0	0	0	0	0	0	0	0	0
Lampyridae	96	202	66	27	6	6	8	4	3	3	4	11	42	31

Appendix *(Continued)*

		1993*							1994					
Invertebrate name	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov
Bostrychoidea														
Bostrychidae	0	4	0	0	0	0	0	1	0	0	0	0	0	0
Cleroidea														
Cleridae	0	0	2	2	0	0	0	0	0	0	0	0	0	0
Melyridae	0	0	0	3	0	0	2	0	0	0	0	0	0	0
Cucujoidea														
Nitidulidae	203	247	198	68	19	36	51	24	11	5	19	36	87	90
Cucujidae	0	137	13	4	4	5	8	3	0	0	1	36	15	11
Cryptophagidae	154	916	27	8	10	22	934	1463	1142	537	217	167	93	35
Biphyllidae	0	0	0	0	0	0	0	0	0	0	0	0	3	3
Endomychidae	0	1	2	6	6	4	3	1	0	0	0	0	0	0
Discolomidae	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Lathridiidae	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Colydiidae	1	2	5	1	0	4	0	0	1	0	0	0	3	1
Tenebrionidae	86	148	40	11	7	5	4	1	4	3	2	0	12	9
Scraptiidae	1	17	11	3	2	0	5	2	4	2	3	22	26	24
Anthicidae	0	7	8	2	1	0	0	0	0	0	0	2	0	1
Aderidae	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Chrysomeloidea														
Chrysomelidae	29	81	20	25	13	2	13	3	3	4	3	1	2	4
Curculionoidea														
Curculionidae	336	677	372	322	545	429	329	55	38	46	35	117	255	312
Scolytidae	145	1280	65	19	5	5	2	1	0	0	0	23	106	131
Coleoptera larva	500	1497	935	769	1247	675	220	73	126	92	63	117	328	238
Siphonaptera	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Lepidoptera														
Psychidae	115	151	21	10	94	153	114	53	40	21	22	37	40	71
Lepidoptera larva	68	175	15	31	53	126	279	134	44	27	16	28	40	38
Lepidoptera: Butterfly	0	0	0	0	2	6	2	0	0	0	0	0	0	0
Lepidoptera: Moth	1	2	1	0	1	0	1	0	1	1	1	2	4	2
Hymenoptera														
Symphyta														
Tenthredinidae	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Apocrita: Parasitica														
Ichneumonidae	3	6	7	4	1	6	12	11	21	6	0	1	4	3
Braconidae	1	31	20	30	23	26	15	5	6	4	1	1	8	8
Proctotrupidae	0	0	0	4	4	2	0	0	2	0	0	0	1	0
Cerapronidae	0	121	21	32	25	12	8	6	0	0	0	1	3	10
Diapriidae	19	99	39	44	49	54	26	13	15	8	4	17	25	17
Scelionidae	32	39	18	23	17	11	11	7	4	1	0	6	25	45
Torymidae	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Pteromalidae	0	2	0	2	0	0	0	1	0	1	0	0	0	0

Appendix *(Continued)*

	1993*			1994										
Invertebrate name	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov
Eulophidae	1	1	0	0	6	3	5	2	2	0	0	0	0	0
Elasmidae	0	2	0	2	0	0	0	0	0	0	0	0	0	0
Mymaridae	0	3	16	8	5	0	4	2	0	1	2	2	5	7
Aculeata														
Mutillidae	0	0	0	0	0	2	0	0	0	0	0	0	0	0
Pompilidae	0	1	2	5	5	2	0	0	0	1	0	0	0	0
Sphecidae	0	0	0	0	1	0	1	0	0	0	0	0	1	1
Halictidae	0	2	2	2	0	0	0	0	0	0	0	0	0	0

* The 1993 values include abundance values from chapters I, II, and III, while the 1994 values were from chapter III. A total of 1 126 invertebrate morphospecies were captured (this value included carabid and ant species from chapters I, II and III.