The Influence of Area Reduction and Commercial Forestry on Epigaeic Invertebrate Communities of Afromontane Forest in the KwaZulu-Natal Midlands

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Preface

This study was carried out in the School of Botany and Zoology, Forest Biodiversity Programme, University of Natal, Pietermaritzburg, from February 1996 to October 2001, under the Supervision of Prof. M. J. Lawes.

The study represents original work by the author and has not been submitted in any form to another University. Where use was made of the work of others, it has been acknowledged in the text.

The chapters of the thesis are written in accordance with the required format for submission to the journal *Biological Conservation*. The chapters depart from this format in the following areas: 1) tables and figures appear in the text and not on separate sheets at the end of each chapter, 2) one acknowledgements section is provided at the beginning of the thesis, and 3) "et al." is italicised in the text.

SIGNED.

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ABSTRACT

This study investigates the effects of forest fragmentation and matrix type on the diversity and distribution of epigaeic invertebrates in selected Afromontane forests of the KwaZulu-Natal midlands. The consequences of area reduction and matrix transformation, due to commercial forestry, for epigaeic invertebrate diversity, and the role of small forest fragments in their conservation, are particularly examined. Data are used to provide guidelines for the management and conservation of Afromontane forest and adjacent land use.

Epigaeic invertebrates were sampled using pitfall-trapping quadrats set along gradsect lines in eleven Afromontane mistbelt mixed *Podocarpus* forests, five of which were surrounded by commercial pine, and five surrounded by the natural grassland matrix. The two sets of five forests were approximately matched in pairs by area (0.5ha to 215ha) and compared for differences in the epigaeic invertebrate communities to determine potential effects of fragmentation and landscape transformation on these communities. A large tract of forest (Leopards Bush Private Nature Reserve, 705ha, hereafter Leopards Bush) situated within the continuous Karkloof forest, served as the control. Trapping intensity increased with forest area. Invertebrates were identified to morphospecies, and where possible, further identification was carried out by specialists.

A total of 61 282 epigaeic invertebrates, representing 168 morphospecies, were collected. There was a significant positive species-area effect evident in the Balgowan complex (grassland matrix), but not in the Gilboa complex (pine matrix). There was thus a confounding influence of the pine matrix in the Gilboa, since the matrix represented the single most important difference between the two forest complexes. In afforested landscapes it is thus crucial to conserve the largest intact forest fragments to preserve overall epigaeic invertebrate species richness.

Density compensation was evident in the Balgowan complex but not in the Gilboa complex. Recolonisation dynamics may play a small role in the regional persistence of a species within forest in a pine matrix, and persistence would be ensured by the preservation of a small number of large forest fragments containing large, extinction-resistant populations. The establishment of ecologically functional grassland corridors (i.e. wide enough to maintain "natural" ecological processes) between mistbelt mixed *Podocarpus* forest fragments would facilitate dispersal of epigaeic invertebrates between forest fragments.

The results of this study indicated that edge effects were experienced deeper in the forests than the expected 32m suggested by Kotze and Samways (1999) and thus any changes to the epigaeic invertebrate communities induced by edge effects had already taken place in these forests.

Cluster analyses revealed that twenty-two percent (n = 37) of invertebrate species recorded were common to all forests and these shared species were generalist feeders. The effect of matrix type on diversity of epigaeic invertebrate communities was most notable for large forests (i.e. over 30 ha). Large fragments with core areas unaffected by edge-induced disturbance would support more forest dependent species than small fragments due to a lower susceptibility to invasions.

Although not significantly nested, epigaeic invertebrate communities in both forest complexes tended toward nestedness. Isolation of forest fragments appeared to play a lesser role than patch area in determining the invertebrate community composition. Assuming that communities are extinction-dominated, community convergence in small fragments has probably already occurred, with invasions from the matrix confounding patterns of deterministic extinction of forest-dependent epigaeic invertebrate species.

A habitat disturbance gradient was evident from the relatively undisturbed control (Karkloof quadrats) to the more disturbed pine dominated Gilboa quadrats, with intermediate disturbance values for the Balgowan (natural grassland matrix) fragments. The undisturbed Karkloof forest was characterised by a deep, abundant leaf litter layer, dense sub-canopy, and an abundance of seedlings indicating high rates of natural regeneration. Leaf litter depth was the most important variable in explaining the variation of epigaeic invertebrate species. A "shopping basket" of eight selected ecological indicators are mostly unrelated species. In general, this study supports the wealth of evidence advocating the use of epigaeic invertebrates, especially Carabid and Staphylinid beetles, as ecological indicators. In this study, eight species were identified by canonical correspondence analysis as ecological indicators that were sensitive to forest disturbance. This suite of species in the mistbelt mixed *Podocarpus* forests of the KwaZulu-Natal midlands will provide an accurate indication of forest condition in summer when abundance data is used.

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CHAPTER 1

Introduction

Over the last two decades South Africa has made the transition from a net importer to a net exporter of forest products with an industry of international size and competitiveness (NFAP secretariat, 1997). The province of KwaZulu-Natal contains 37% of South Africa's total commercial plantations, with afforestation occurring at a rate of 10 000 to 12 000 ha per annum. Along with the Eastern Cape, KwaZulu-Natal still has the greatest potential for further afforestation in South Africa (NFAP secretariat, 1997).

Afromontane mistbelt mixed *Podocarpus* forest (hereafter: mistbelt forest) forms the largest component of the indigenous forest biome in KwaZulu-Natal, and many of these naturally fragmented forests are now surrounded by commercial plantations. Very little work has been done to assess the impact of this fairly recent (± 100 yrs) conversion of the natural grassland matrix to commercial plantations on forest dependent fauna and flora in KwaZulu-Natal.

This project addresses this issue using epigaeic invertebrates living in indigenous mistbelt forest patches. The purpose of this project is to gain an insight into some of the ecological processes occurring in mistbelt forest and to generate new ways of managing and conserving these indigenous forests.

1. History of indigenous and commercial forest

1.1. Commercial forestry

Commercial forestry in South Africa dates back approximately 100 years. In 1914, at the start of World War I, the South African government owned 22 500 ha of commercial plantation. During the second World War private enterprise began processing timber, increasing the amount of hardwood produced from 226 500 m^3 at the beginning of the war to 2 226 000 m^3 in 1944 (Van der Zel, 1989). In 1996/7 1.3% of South Africa was under plantation, producing 18,641 million m^3 of wood, with KwaZulu-Natal producing 40% of this (7,506 million m^3) (Department of Water Affairs and Forestry, 1996). Furthermore, in 1989 the KwaZulu-Natal midlands and coastal catchment areas had a total afforested area of 154 100 ha, which accounted for 13.3% of the total catchment area in the region (Van der Zel, 1989). In 1996/7, this figure rose to 577 788 ha, 38.1% of the total afforested area of South Africa (Department of Water Affairs and Forestry, 1996).

Currently, one of the main threats to ecosystems is the fragmentation of natural habitat due to human expansion. As human populations grow natural landscapes are

increasingly altered due to commercial, agricultural and urban development. The problem of increasing conversion of natural landscapes to commercial forestry is summarised by Grey (1989): "Multiple landuse as a policy and approach has received only lip service in the rush to convert vacant hectares to exotic eucalyptus and pine species. Disturbing trends are presently underway as the industry finds it far more cost effective to plant grasslands than to convert old wattle, pine and gum stands. Conservation of the resource base has become a secondary priority as inputs escalate and we follow trends fashioned by agriculture."

1.2. Indigenous forest

Afromontane forest appears to have maintained its present general location for the last 12 000 years, since the end of the last glacial maximum (Lawes, 1990). Periodic expansions and contractions of the forests resulted from climatic conditions brought on by glacial and interglacial events that characterised the Pleistocene and Holocene. During the last glacial maximum the area occupied by Afromontane forest would have been at a minimum due to the intensification of cold trade winds and the prevalence of dry, subsiding air masses, among other factors (Tinley, 1985; Lawes, 1990). As climate warmed after these dry conditions, warm moisture laden air coming off the sea and the proximity of the escarpment to the KwaZulu-Natal coast would have combined to bring about orographic rainfall (Lawes, 1990). Fire protected sites would have been abundant in the region, and this may have facilitated the re-establishment and expansion of Afromontane forest, accounting for the numerous small forest blocks found in the region today (Cooper, 1985).

In Fourcade's (1889) report on the forests of the Natal colony, he described their condition as "deplorable." Prior to the arrival of white settlers, the Nguni people relied on large quantities of wood for fencing, fuel, huts and kraals. Further damage occurred through the practise of wintering their cattle in indigenous forests (McCracken, 1986). Early white settlement (pre-1840) in the Natal colony had only a localised effect on forest land due to the sparse settler population (McCracken, 1986). Some logging for timber took place in Karkloof, Nottingham Road and the immediate surrounds of Pietermaritzburg and Port Natal (Durban) (McCracken, 1986). The Voortrekker Volksraad encouraged the use of local timber by imposing an import duty of 25% on all wood and wood products not locally produced (McCracken, 1986). The British annexure of the Republic of Natalia in 1843 marked the beginning of the gross exploitation of the forests in Natal. By the 1860's Durban's local supply of timber was so diminished that the port had to rely on imported timber or timber brought in from the Boston and Karkloof forests. Approximately 14 million cubic feet of timber was removed from the Karkloof forest alone in the 1860's (McCracken, 1986). During this decade a number of sawmills appeared in the Natal midlands forests. Sawyers, consisting mainly of ex-soldiers and sailors, ravaged many forests the in Natal colony. Rycroft (1944) mentions an eyewitness account of a convoy of 76 wagons loaded with timber from Karkloof heading for the Transvaal after gold had been discovered in the 1870's. By the 1880's Durban alone was

using 6 000 tons of timber for fuel annually (McCracken, 1986). The Ingeli forest (near Kokstad) is one forest that fell prey to both sawyers and sawmills. Fourcade (1889) wrote "The Ingeli must have once been a magnificent forest... It is deplorable to see how ignorant and ruthless working has contrived to ruin a large portion."

The need for timber for fuel by the people of Pietermaritzburg also had a profound effect on forests in the area. The Swartkop forest near Pietermaritzburg was reduced from 3 237 ha in the late 1800's (Fourcade, 1889) to its current area of 176 ha (Cooper, 1985). It is likely that, given estimates of both Fourcade (1889) and Rycroft (1944), the Karkloof forest suffered a reduction in area of between 24% and 50%, and possibly as high as 70% during the mid- to late-19th century (Lawes, unpublished manuscript). Logging ceased in these forests in the 1940's, and the consequences of this exploitation for the forest fauna and flora are still not known.

2. The forest biome and associated biodiversity

The forest biome covers 0.2% of South Africa's land surface, approximately 400 000 ha (NFAP secretariat, 1997), yet contains 5.5% of South African plant species which makes it the second richest biome in South Africa after the fynbos biome. It also contains 14.1% and 14.2% of the South African mammal and bird species respectively (Geldenhuys and MacDevette, 1989). Fifty bird species, 76 butterfly species, 12 reptile species, 8 amphibian species and 28 mammal species are forest dependent, while 57 bird species, 136 butterfly species, 57 reptile species, 28 amphibian species and 143 mammal species are associated with the forest biome (Forest Biodiversity Programme database). The forest biome contains 16.4% of the endemic faunal species of Southern Africa. Only 58.8% of mistbelt mixed *Podocarpus* forests in KwaZulu-Natal are protected (Geldenhuys and MacDevette, 1989). These facts alone make the forest biome a conservation priority, yet these forests are poorly conserved and there has been little or no effort to determine those processes important in maintaining this wealth of animal and plant life.

2.1. Characteristics of mistbelt mixed Podocarpus forest

Edwards (1967) described the climatic climax forest vegetation of the KwaZulu-Natal mistbelt region as Mistbelt Mixed *Podocarpus* Forest in his survey of the Tugela Basin. Previously this forest type has been called High Timber Forest (Fourcade, 1889), Yellow Wood Bush (Bews, 1912) and Temperate Forest (Pentz, 1945; Acocks, 1953). This forest type occurs throughout KwaZulu-Natal and the Eastern Cape, between 1 000 - 1 500 m ASL, where summer rainfall ranges from 700 mm–900 mm, and temperatures reach a maximum of 40°C (Moll, 1969; 1976). The forests are situated in fire-protected sites on steep south-facing slopes (Moll, 1976; Geldenhuys and MacDevette, 1989). Mistbelt forest covers a total area of 30 868 ha (Cooper 1985) in KwaZulu-Natal, representing 34% of the total indigenous forest

areas in the province. The canopy of mistbelt forest is between 14-27 m tall (Moll, 1976), with *Cassipouria gummifolia, Rapanea melanophloeos, Afrocarpus henkelii, Xymalos monospora* (Everard *et al.*, 1995), *Calodendrum capense* and *Celtis africana* (Moll, 1976) as the common species. Other species associated with this forest type include *Ptaeroxylon obliquum, Olea capensis, Cussonia chartacea, Cryptocarya myrtifolia, Prunus africanus, Kiggelaria africana* and *Combretum kraussii* (Moll, 1969).

These forests are fine-grained (Everard *et al.*, 1995), which means that the composition of the sub-canopy is very similar to that of the canopy. Both strata consist primarily of shade-loving seeders (Everard *et al.*, 1995), resulting in few large trees compared to the number of saplings which grow into gaps created by tree-falls. The shrub layer reaches up to 4 m tall, and under this is usually a well-developed layer of grasses and sedges. Numerous herbs, often forming a continuous layer, are also present (Moll, 1976).

The mistbelt forests of the Karkloof / Gilboa / Balgowan region in KwaZulu-Natal have a median area of 0.29 ha (n = 1 277). Some 75% of these forests were smaller than 0.5 ha in 1944 (Cooper, 1985; Van der Zel, 1988), and while many of these have since been eliminated, a large proportion of small fragments has persisted (MacFarlane, 2000).

As these fragments are situated in a disturbed, agro-commercial landscape, they are subject to a number of threats to their survival, including exposure to burning, invasion by livestock, afforestation and wood removal. A large amount of this forest type is privately owned (14 573 ha) and these forests are generally not well protected (Cooper 1985).

3. Impacts of commercial forestry on biodiversity

The impacts of commercial forestry on biodiversity associated with mistbelt forest have been poorly studied in KwaZulu-Natal. According to Macdonald (1989) afforestation and alien tree invasion are two of the eight major land transformations that negatively affect the native biota in South Africa. Karr (1990) suggests that spatial configuration of habitat patches is particularly important because recolonisation following area-dependent faunal extinctions is not assured merely by the presence of a large mainland source. As recolonisation of habitat islands depends on the dispersal ability of potential colonisers, the nature of the surrounding matrix as well as the spatial configuration of the habitat fragments is important. This was illustrated by Powell and Powell (1987) who showed that male euglossine bees, which function as pollinators in Amazonian forest fragments, failed to cross narrow (100m) cleared areas, possibly because of altered microclimatic conditions. Commercial plantations typically surround or are immediately adjacent to large areas of indigenous forest.

The effect of plantations on biodiversity in neighbouring habitats has not been extensively studied. However, the species richness and abundance of plants, birds and small mammals were much greater in indigenous forest habitat than in mature pine plantations of similar area at Jonkershoek, near Stellenbosch in the Cape Province, South Africa (Scott, 1978; Richardson and van Wilgen, 1986; Armstrong and van Hensbergen, 1994). Commercial

forest may act as a selective filter to organisms moving between forest fragments. Selective filters are dispersal routes containing a limited habitat spectrum through which certain species pass and others are excluded (Noss, 1991). Winterbottom (1968) showed that plantations in the fynbos biome were depauperate in bird species when compared to indigenous habitats in the same region. In addition, bird species richness and population densities were found to be lower in pine stands than in riparian habitat at Jonkershoek (Armstrong and van Hensbergen, 1994). Samways and Moore (1991) have noted that the presence of pine species caused a reduction in local grasshopper species richness and abundance in grasslands. Samways *et al.* (1996) further showed that invertebrate species richness was greatest in sites dominated by trees (as opposed to grassland), and that sites with exotic trees had lower species richness than those with indigenous trees.

Some species, on the other hand, are able to use the matrix and extend their ranges when habitat is altered. Allan and Tarboton (1985) documented the range expansion of four *Accipiter* species facilitated by the planting of commercial trees and the invasive spread of these exotic trees along watercourses. Most of the nests of these raptor species were found in exotic rather than indigenous trees.

In spite of a number of negative impacts it is worth noting that commercial forestry has also provided an alternative to using indigenous timber that almost certainly rescued many indigenous forests in the province from forestry practises in the early 1900's.

4. Ecological consequences of fragmentation of forest habitat

The negative effects of fragmentation on species richness arise in part because of the effects of reduced population size and should be evident even in those species that do not become extinct. For habitat specialists restricted to fragments and unable to use the matrix, density in fragments would be reduced due to increased demographic stochasticity and disruption of metapopulation dynamics (Debinski and Holt, 2000). Alternatively, robust or generalist species may move from the matrix into the remaining habitat fragments, resulting in species crowding in these fragments (Debinski and Holt, 2000). Debinski and Holt (2000) found evidence supporting increasing species richness with area in six out of fourteen studies that had set out to investigate this pattern. Even in a 100 ha tropical forest fragment, a beetle community was recognisably different in composition and lower in species richness than those on control sites in continuous forest (Laurance and Bierregaard, 1996). Collinge (1995) found that insect species diversity was lowest in the smallest fragments and highest in the largest fragments. In a comparison of several species of grassland insects, Collinge and Forman (1998) found that large bodied, initially rare species, were concentrated in the remaining larger core habitats, as opposed to areas where a central portion of habitat was removed. Debinski and Holt (2000) report a similar decrease in arthropod species richness with increasing fragmentation of an old field and determined that the pattern was driven primarily by the loss of rare species. In an old field study in Kansas (Holt *et al.*, 1995a, 1995b;

Robinson *et al.*, 1992) larger patches had higher species richness of butterflies, but small mammals and plants tended to show less consistent differences in species richness among patch sizes.

Debinski and Holt (2000) further noted that the effects of habitat fragmentation might be mediated or exacerbated through shifts in individual species behaviour and interspecific interaction such as predation. Kareiva (1987) demonstrated this effect by experimenting with an aphid and a coccinelid predator in monocultures of *Solidago*. The fragmented treatment had more frequent aphid outbreaks, apparently due to the inability of the predator to aggregate rapidly at localised clusters of the aphid in early phases of the outbreak. Didham *et al.* (1998), while investigating beetle species responses to tropical forest fragmentation, found that estimated species loss from forest fragments was of the order of 49.8% of common species from 1 ha fragments, 29.8% from 10 ha fragments, and 13.8% from 100 ha fragments. In their study, beetles represented 11% of the total invertebrate abundance and included fungivores, herbivores, predators, saprophages, xylophages and xylomycetophages (specialists on *ambrosia* fungus inside wood). Their study showed that declining density was a significant precursor of species loss from forest fragments, while some species that did not show population density responses to fragmentation were also absent from some fragments, presumably by chance.

Although this study did not specifically test the predictions of the equilibrium theory of island biogeography, a general overview of the theory is warranted in the light of the fragmented and isolated nature of the forest fragments under study.

Species-area theory was based upon the equilibrium theory of island biogeography (Preston 1960; MacArthur and Wilson 1963, 1967). In its most basic form the species-area relationship is a monotonic increase in the number of species with increase in area for a set of sites (Williams, 1964; Simberloff, 1992). This relationship is explained by the equilibrium theory of island biogeography as the outcome of local extinction of species already on the island and the immigration of species from source areas to the island (Simberloff, 1992). The number of species on an island remains constant but in dynamic equilibrium since turnover or replacement of species continually takes place. In general, larger islands contain more species because they have larger populations that are less vulnerable to deterministic (e.g., area dependent) or stochastic (e.g., disease, climatic catastrophe) extinction effects (Pielou, 1977; Dennis *et al.*, 1991).

In the absence of tests of the predictions of the equilibrium theory of island biogeography, species-area analyses should be used cautiously, if only because a positive species-area relationship may not represent an equilibrium state. The assumption of stable species equilibrium in the use of species-area theory has been questioned on two further points. First, in natural systems the environment is continually changing, often with pronounced effects on populations (Chesson and Case, 1986), and species assemblages are unlikely to achieve a stable equilibrium. Secondly, the species in many communities do not appear to have many of the attributes necessary (e.g., ability to survive changing conditions

and perturbations) for stable species equilibria (Chesson and Case, 1986). In the above cases, populations are in a state of non-equilibrium.

Habitat fragmentation affects distribution patterns of those species that occur in them (Willis, 1979; Burgess and Sharpe, 1981; Blake and Karr, 1987). Often in a given set of replicate habitats with biotas varying in species richness, less species rich biotas tend to be subsets of more species rich biotas (Cutler, 1991; Whittaker, 1992). A high overlap in species composition therefore exists among sites, such that smaller biotas tend to be made up of the same species, while larger biotas contain these species plus others not found in smaller assemblages (Cook, 1995). Patterson and Atmar (1986) termed this pattern of species distribution the "nested subset" concept, and this has received increased attention from ecologists over the past decade (Patterson and Atmar, 1986; Cutler, 1991; Patterson, 1987; Patterson and Brown, 1998; Wright and Reeves, 1992; Atmar and Patterson, 1993; Doak and Mills, 1994; Wright *et al.*, 1998).

Density compensation usually describes an inverse relationship between population density and species richness (McGrady-Steed and Morin, 2000; Stevens and Willig, 2000). However since species richness is a positive function of area, if we assume that the density of a group of species is constant per unit area, then the individual species must, on average, decrease in larger areas (Schoener, 1986). Density compensation may thus be a natural corollary of density-area effects. MacArthur *et al.* (1972) found that island species generally had higher population densities than mainland species in the Pearl Archipelago off Panama. They suggested that species on small islands were subjected to lower levels of interspecific competition and predation, which allowed their populations to increase. However Schoener (1986) and Connor *et al.* (2000) argue that if total species density is independent of area, and if a species-area relationship exists, one need not infer competitive release to account for density compensation.

With the above in mind, this project assesses the impacts of both the reduction of forest area and its isolation on epigaeic invertebrate communities. It further estimates disturbance and its effect on epigaeic invertebrate communities in each forest, as well as assessing the degree to which commercial forestry (*Pinus patula*) affects epigaeic invertebrate diversity.

5. Objectives

i.   To investigate the current conservation and management status and diversity of epigaeic invertebrates in selected Afromontane mistbelt mixed *Podocarpus* forest.

ii.   To examine the consequences of area reduction and matrix transformation due to commercial forestry on the diversity of epigaeic invertebrates, and assess the role of small forest fragments in their conservation.

iii.   To use data to provide guidelines for forest conservation and adjacent landuse

planning.

6. Hypotheses

In this dissertation I primarily test the following hypotheses:

i.   Commercial forestry has a negative impact on the epigaeic invertebrate species diversity in indigenous forests that are historically surrounded by a grassland matrix.

ii.   Although epigaeic invertebrate species richness itself may not be severely affected by matrix type, assemblage composition and species abundance will be.

iii. Non-equilibrium models of island biogeography can largely explain the community structure within these forest fragments, with deterministic extinctions occurring.

iv.   Community structure and species assemblages within forests result from deterministic extinctions as mistbelt forest area decreases. Species assemblages become more similar with decreasing forest area as those more resistant to extinction persist in the smaller forests. These species assemblages are subsets of those found in larger mistbelt forests (Nested subsetting, Cutler, 1994).

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CHAPTER 2

Sampling design and non-analytical methods

1. Study site and sampling methods

1.1. Study site and selection of forest fragments

See Chapter 3, section 2.1.

1.2. Sampling methods

See Chapter 3, section 2.2.

1.3. Selection of taxa

Invertebrates are highly sensitive to modifications of habitat and, due to high abundances, are much more amenable to statistical analysis than vertebrates (Collins and Thomas, 1991; Kremen 1992; Kremen *et al.*, 1993). Furthermore, they provide the researcher with a vast amount of data fairly rapidly due to their abundance and the ease with which they are sampled, both passively and actively. While this may be seen as an advantage, processing such large data sets is a formidable task (Kremen *et al.*, 1993; Samways, 1994). Identification to the species level most often requires the attention of specialists. Without species identification the life-histories of the invertebrates under study are unknown. This poses problems when functionality and ecological roles are required for interpretation. To address these problems, specialists within the University of Natal and the Natal Museum were used to identify those groups with which they were familiar to the family level (and further where possible). These were the flies, ants, wasps, bees, millipedes, snails and slugs. The author identified the beetles to the family level.

Putman (1994) suggests that invertebrates, as entire assemblages or as components within a community of mixed assembly, might be strongly influenced by stochastic processes, showing little temporal or spatial stability. Generation times are relatively short and populations will immediately respond to any pressure from environmental perturbations. Invertebrates will therefore reflect processes currently occurring in the forests. This may create problems with temporal factors like seasonality and physical factors such as disturbance affecting or confounding results. In this study intensive and continuous trapping during the summer months (December - March) controlled for the effect of seasonality. Differing levels of disturbance in forest fragments were calculated and factored into analyses to isolate area and matrix effects. The method used to obtain a plant-based index of

disturbance is discussed later (Chapter 5).

Terrestrial invertebrates have been used as bioindicators in a number of different habitats and environmental scenarios (Holloway *et al.*, 1992; Rosenberg *et al.*, 1986; Kremen *et al.*, 1993). Forest studies have included the use of single species, higher taxa, assemblages and communities of, for example, dragonflies, tiger beetles, ground beetles, moths, butterflies, sawflies and ants, in habitats such as forests, grasslands, sand dunes, urban areas and mine sites (McGeogh, 1998). Epigaeic invertebrates are an appropriate bioindicator group in multi-taxa conservation orientated studies like this one for several reasons: 1) they include some of the most studied terrestrial taxa e.g. carabid beetles and ants; 2) they play an fundamental role in maintaining ecosystem processes (Chapman *et. al.*, 1988; Giller 1996), such as nutrient cycling and predation; and 3) data on this group are easily collected using pitfall trapping techniques (Samways *et al.*, 1996).

2. Sampling regime

2.1. The use of the gradsect method in sampling design

The sampling strategy for a survey of any part of the living resource must balance the cost of logistic input against the value of information output (Gillison and Brewer, 1985). Financial and time constraints, and the increasing demands for for manageable resource data therefore provide good reasons for optimizing sampling methods.

The distribution of living things is influenced by the distribution of environments rather than by systematic or random phenomena (Gillison and Brewer, 1985). It follows that the application of statistically based survey designs that employ systematized or completely random models may not accommodate underlying non-random distribution of biota and may fail to detect natural patterns. Sampling methods should incorporate as much of the potential habitat heterogeneity within the sites as possible in order to obtain a more accurate assessment of the actual diversity of the biota within the respective habitat types (Gillison and Brewer, 1985). For this reason I used the gradsect method (Gillison and Brewer, 1985) in this study. Gradsects are non-random transect lines orientated to sample the most significant potential environmental gradient in the site (Gillison and Brewer, 1985). Oliver and Beattie (1996a) adopted the gradsect approach as a cost -effective method of surveying invertebrates, and Austin and Heyligers (1989) used this approach for a vegetation survey of forests in North-eastern New South Wales, Australia. Gillison and Brewer (1985) compared the effectiveness of the gradsect method to normal transect methods in determining vegetation richness in an area of 424 km^2 in southern Australia. Their results show that the gradsect method recovered 21% more patch richness than random transects of equal length.

As distance from the forest margin increases, edge effects decrease (Laurance and Yensen, 1991). Edge effects form a gradient associated with physical and biotic changes in all habitat fragments (Angelstam, 1992; Laurance and Yensen, 1991). Forest edges generate

microclimatic gradients that produce an environment that is different from both the matrix outside the forest and its interior (Angelstam, 1992). Within the forest fragments, gradsect lines were run from the forest margin into the forest interior and up the slope to incorporate any physical and biotic variation due to edge effects or small altitudinal differences. These gradients were perceived to be the gradients of importance to biodiversity in the fragments (Gillison and Brewer, 1985).

2.2. Sampling strategy

All forest fragments were sampled over two seasons. The first season was a pilot season, to build up a reference collection for the invertebrates, and to test whether the originally selected and sampled taxa (lepidopterans, epigaeic invertebrates and small mammals) would yield results that could be used for the purposes of this study. Also, this season was used to determine sampling strategy. In the second sampling season, density estimates were obtained for the taxa that were selected from the first season. Small mammals and epigaeic invertebrates were sampled in the second season, but lepidopterans were not due to difficulty in identification in the field and obtaining density estimates for the populations. Small mammals were not included in this thesis as all species recorded proved to be generalist species, found in all the forest fragments. Species abundance was not measured, and small mammals provided poor discriminatory power in terms of disturbance resulting from either forest area or matrix type.

2.2.1. Sampling epigaeic invertebrates: Season 1

During the first sampling season (1996/1997) epigaeic invertebrate species richness was estimated for each of the 11 forests. Three gradsects, each of 200 m length, were laid out in the Karkloof forest, separated by a minimum distance of 200 m Trapping stations were 10 m apart along the first gradsect, 15 m apart along the second gradsect, and 20 m apart along the third.. Trapping stations consisting of three pitfall traps, one baited lepidopteran trap and one small mammal trap, were set up along the gradsects. This was done primarily to determine the effect of sampling intensity on estimates of biodiversity, but also to establish the best use of the available traps and sampling time available. All three gradsects were found to yield similar numbers of species (10 m -79; 15 m - 75; 20 m – 72). Community structure was also very similar, with the 10 m interval and 20 m interval transects being more similar (63 %; Jaccard similarity measure) than either the 15 m interval and 10 m interval (57%) or the 15 m interval and 20 m interval transects (61%). An interval of 20 m between trapping stations was therefore used for sampling the Gilboa and Balgowan forest fragments for both the first and second sampling seasons.

2.2.2. Sampling epigaeic Invertebrates: Season 2

In the second field season (1997/1998) diversity and density estimates were obtained for the epigaeic invertebrates in each forest. Trapping was done along the gradsect lines used in the first sampling season. Trapping stations were placed 20 m apart, and comprised a 3 m x 3 m quadrat with 16 pitfall traps each 1m apart (traps were placed at the corners of the quadrat).

The pitfall trapping technique (Majer, 1978) has been used successfully by many ecologists for a wide variety of invertebrates (Corey and Stout, 1992; Kotze and Samways, 1999; 2001; Samways *et al.,* 1996; Steinberger, 1991; Stiles, 1985; Olson, 1991; Oyediran *et. al.,* 2000; - but see Marsh, 1984), and is useful for collecting a large amount of data fairly rapidly (Samways *et al.,* 1996). Pitfall trapping is more objective and consistently reliable than searching techniques (Samways *et al.,* 1996), especially when one is not targeting a specific or visually obvious taxon. The traps in this study were deliberately not baited so that species composition and richness data were collected from a random sample of epigaeic fauna occurring in the forests. However, the preservative mixture that was used in the pitfalls may have attracted certain invertebrates (and conversely repel others) as was shown by the presence of invertebrates that use flight as their preferred means of mobility, such as flies and most of the hymenopterans. These factors may lead to biased sampling, and need to be looked at in greater detail. On the other hand, the pitfall method allows for standardisation and comparative interpretation (Duelli *et al.,* 1999), as well as density estimation of target groups. Another advantage of pitfall trapping methods is the capture of cryptic and nocturnal animals that are not commonly captured by searching techniques (Samways *et al.,* 1996).

3. The morphospecies concept

Identification to the morphospecies level provides species numbers with a fair degree of accuracy and consistency (Oliver and Beattie, 1996b), and may even give an insight to functional roles, but at least some level of expertise is required to obtain any degree of accuracy. One way around this dilemma is to select indicator groups, or more precisely, biodiversity indicator groups (McGeoch, 1998), thus enabling specific questions to be answered while reducing the number of species processed. Even so, with the vast array of species little ecological information is known about many of them. This is further complicated by the fact that many invertebrate species undergo morphological and also ecological changes associated with their life-cycles. Indicator groups therefore need to be selected very carefully and need to be taxonomically well known (Samways, 1998).

The invertebrates from each sample were sorted into morphospecies (Oliver and Beattie, 1996b) based on gross morphology, size and colour using a normal magnifying glass. This method may have resulted in 'splitting' (Oliver and Beattie, 1996b), i.e. the division of one species into several different morphospecies due to sexual dimorphism, colour variation, or

variation in body size, and results in overestimates of species richness. To control for this bias the hymenopterans (ants and wasps), the molluscs and the millipedes were identified to the species level by specialists. The beetles were identified to the family level (and further where possible) by the author. Where there was lumping of samples, these were removed from analyses, and in cases of splitting, same-species that had been split into different morphospecies were grouped. Rosenberg *et al.* (1986) caution against using morphospecies in population and community analyses, suggesting that to gain an understanding of the nature of changes in invertebrate community structure, identification to the species level is essential.

Supporters of the use of functional approaches have two concerns: (a) that the presence of a high number of species results in functional and structural redundancy, and (b) that it is impossible to study all species, especially in a group as diverse as the insects. Oliver and Beattie (1996b) advocate the careful use of morphospecies in the interest of cost-effectiveness, and showed that results for species richness obtained from sorting ants, spiders and beetles were largely consistent, whether animals were sorted to species by specialists, or to morphospecies by non-specialists. Identification to the morphospecies level for groups other than the ants, beetles, wasps, snails and millipedes was necessary due to the number of invertebrates that had to be processed (n = 61 282), and due to the cost involved in identifying invertebrates to the species level. Also, the comparative nature of this survey allowed an approximation of species richness, as the errors in these estimates were assumed to be consistent over all fragments sampled.

In all analyses where abundance measures were required, the total number of captured invertebrates per quadrat was obtained, and median values per week and per forest were used. Where species existed in the forest or quadrat and the median value was zero, a representative value of one replaced the zero.

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CHAPTER 3

Investigating patterns of epigaeic invertebrate community structure in a fragmented mistbelt mixed Podocarpus forest environment

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Abstract

Mistbelt mixed *Podocarpus* forest in the KwaZulu-Natal midlands has been fragmented for at least the last 12 000 years. In the last 100 years much of the historical grassland matrix between indigenous forest patches has been replaced by commercial forestry, mainly pine (*Pinus patula*) plantation. While the grassland matrix is not without disturbance (fire, livestock grazing), replacement by pine trees considerably alters the landscape ecology. I sampled epigaeic invertebrate communities using pitfall trapping methods in 11 mistbelt mixed *Podocarpus* forests, half of which were surrounded by pine plantation. It is generally held that fragmentation of habitats leads to extinction dominated communities, especially in the case of non-mobile animals such as most epigaeic invertebrates. Thus, the community composition of smaller habitat fragments are predicted to converge because of the deterministic nature of the extinctions, and the low frequencies of recolonisation. Similarity indices and nested subsetting techniques were used to assess the effects of the fragmentation and community isolation on these forests. In addition the influence of the matrix type on epigaeic invertebrate community composition was investigated. All communities shared 22% (37 species) of recorded epigaeic invertebrate species, and cluster analyses showed them to be 60% similar in composition. Epigaeic invertebrate communities were not nested, but tended towards nestedness. This trend extended to individual taxa, indicating that these communities were not extinction or colonisation dominated and that species convergence had most probably already taken place in the fragments with invasions from the matrix confounding the resulting patterns.

Key words: commercial forestry; complementarity; diversity; epigaeic invertebrates; forest; fragmentation; island biogeography theory; matrix effects; matrix temperature; nested subsets; pine.

1. Introduction

The mistbelt mixed *Podocarpus* forests of KwaZulu-Natal have been fragmented and in their present general location for the last 12 000 years (Lawes, 1990). However the area in which these forests are situated has been converted within the last century from a grassland dominated landscape into an agro-commercial zone, consisting of agricultural crops, livestock and commercial forestry. The mistbelt forest fragments that remain are generally small and range between 0.01 and 1685 ha in area (median = 0.29 ha; n = 1277; MacFarlane, 2000) with about 75% smaller than 0.5 ha in 1944 (Cooper, 1985; Van der Zel, 1989). Some 38% of all forests present in 1944, mainly those less than 1 ha, have since been destroyed (MacFarlane, 2000). For animals that rely on Afromontane mistbelt-mixed *Podocarpus* forest, fragments have become increasingly isolated and difficult to colonise successfully. This is largely because of the transformation of the historical grassland matrix by commercial

plantation forestry (and other agricultural crops), but is also due to an increase in disturbance to, and the loss of, existing forests.

Epigaeic invertebrates are an interesting group to study from the point of view of fragmentation effects. In general, invertebrates are small, hyperdiverse and their generation times are short. They are highly sensitive to changes in their environment (Kotze and Samways, 1999; Putman 1994) and respond immediately to any disturbances (Putman, 1994). Invertebrates are thus good indicators of current habitat heterogeneity, ecosystem diversity and environmental stress (Dempster, 1991; Colwell and Coddington, 1994; Weaver, 1995; McGeoch, 1998). Epigaeic invertebrates, the selected target group for this study, make up the majority of the invertebrate fauna in forests and fill a wide variety of functional roles in this ecosystem (Chapman *et al.*, 1988; Samways, 1994). Their success in this fragmented landscape ultimately depends on their ability to survive adverse conditions if they remain in disturbed forest habitats, or their ability to disperse to other, less disturbed, forests.

1.1. The concept of nested subsets: formation and persistence of communities

Habitat fragmentation affects distribution patterns of those species that occur in them (Willis, 1979; Burgess and Sharpe, 1981; Blake and Karr, 1987). Often in a given set of replicate habitats with biotas varying in species richness, less species rich biotas tend to be subsets of more species rich biotas (Cutler, 1991; Whittaker, 1992). A high overlap in species composition therefore exists among sites, such that smaller biotas tend to be made up of the same species, while larger biotas contain these species plus others not found in smaller assemblages (Cook, 1995). Patterson and Atmar (1986) termed this pattern of species distribution the "nested subset" concept, and this has received increased attention from ecologists over the past decade (Patterson and Atmar, 1986; Cutler, 1991; Patterson, 1987; Patterson and Brown, 1998; Wright and Reeves, 1992; Atmar and Patterson, 1993; Doak and Mills, 1994; Wright *et al.*, 1998).

1.1.1. Differential dispersal/colonisation ability

Animals that are able to disperse will colonise areas along dispersal routes in a predictable manner due to differential immigration ability (Cutler, 1994), with more isolated fragments being populated by a subset of more mobile species, and will thus form nested patterns (Patterson and Atmar, 1986). Darlington (1957) called this the "immigrant pattern". The potential for colonisation-driven nestedness (through differential dispersal ability) is suggested by experimental studies of recolonisation by invertebrates of defaunated mangrove islands (Simberloff and Wilson, 1969). Indeed, an archipelagic arthropod community in which immigration was prevented (Rey, 1981) was found to be significantly "anti-nested" i.e. to have species communities that were more heterogeneous than expected by chance (Wright *et al.*, 1998). Of 279 data sets that were examined by Wright *et al.* (1998), ten were consistently

anti-nested and nine of these were arthropod data sets. However, most leaf-litter invertebrates (i.e. epigaeic invertebrates) are unable to move away from and out-distance local disturbances because many species rely entirely upon the resources provided by the organic leaf-litter layer (Hammond, 1990; Holloway and Stork, 1991), and are thus limited in terms of their ability to track environmental change (cf. Thomas, 1994). Consequently, epigaeic invertebrates have to respond to pressure effects *in situ*, and a wider spectrum of species may show a common response to, and reflect current conditions within, the habitat.

1.1.2. Is nestedness a consequence of selective immigration or extinction?

An understanding of the underlying mechanisms generating nestedness is crucial in understanding the ecology of fragmented systems, so that suitable management plans may be applied. Nestedness could result from differential extinction as a function of area, and /or differential colonisation, as a function of isolation of fragments (Lomolino, 1996). However, in terrestrial fragments the causal factors of nestedness include variables such as habitat diversity, disturbance, matrix heterogeneity, matrix tolerance, and edge effects (Forman, 1997). Habitat islands are complex systems in which empirical evidence for causal mechanisms is difficult to obtain without the use of experimental manipulations which serve to isolate one or a few testable variables (Simberloff and Wilson, 1969; Simberloff, 1976). The colonizing potential of a terrestrial organism depends on its mobility. Highly vagile species are able to colonize sites a greater distance from the source area than less vagile species (Cutler in press). Closer biotas (less isolated) would therefore be expected to contain species with a range of dispersal abilities, whereas further, or more isolated biotas would be restricted to mobile species only (Cutler in press). Lomolino (1996) predicted that (i) if community structure is influenced by selective immigration, then the focal system should exhibit significant nestedness when ordered by increasing isolation, and (ii) if community structure is influenced by selective extinction, then the focal systems should exhibit significant nestedness when ordered by decreasing area.

In this chapter I compared the structure of epigaeic invertebrate communities in two terrestrial "archipelagos" or complexes of mistbelt-mixed *Podocarpus* forests, one in a matrix of commercial pine plantation (Gilboa complex), and the other in the historic grassland matrix (Balgowan matrix). I used clustering techniques for this comparison, and also assessed the degree of nestedness of the epigaeic invertebrate communities within the two forest complexes. I investigated the contribution of the potentially dominant processes – selective extinction or colonisation, to forest bird assemblage structure and composition in the forest fragments of the Gilboa and Balgowan forest complexes.

I predicted that mistbelt forest epigaeic invertebrate communities in both pine and grassland matrices would be significantly nested due to the isolation of the forest fragments. I further predicted that less colonisation of epigaeic invertebrates in the pine-surrounded forest fragments would occur due to the inhospitable nature of this matrix habitat further isolating the

forest fragments. These communities were expected to be extinction-driven, and therefore nested to a greater degree than communities in the Balgowan forests that were not surrounded by pine plantation.

2. Method

2.1. Study site and selection of forest fragments

This study was conducted in the Karkloof, Gilboa and Balgowan forest complexes (29°20'S, 30°15'E), situated in the midlands of KwaZulu-Natal province, South Africa (Fig 1). The forests in this area are classified as Afromontane mistbelt mixed *Podocarpus* forest (Edwards, 1967; Pooley, 1993; Cooper, 1985). The mistbelt forests of the Karkloof/Gilboa/Balgowan region in KwaZulu-Natal have a median area of 0.29 ha (n = 1277). Some 75 % of these forests were smaller than 0.5 ha in 1944 (Cooper, 1985; Van der Zel, 1988), and while many of these have since been eliminated, the large proportion of small fragments has persisted (MacFarlane, 2000).
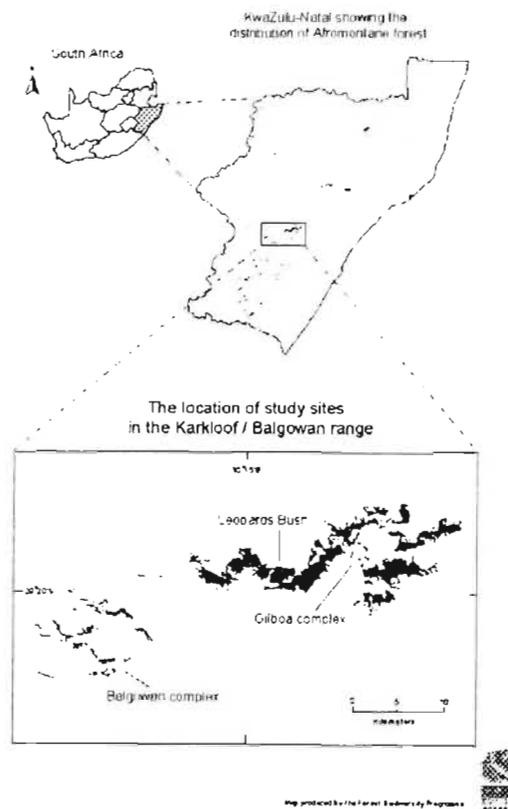
Figure 1. Location of study sites in KwaZulu-Natal.
Map created by the Forest
Biodiversity Programme,University
of Natal, Pietermaritzburg.

In order to assess the influence of a commercial forestry matrix on selected taxa in indigenous forest, five mistbelt forest fragments that were historically (i.e. at least one complete rotation cycle, 12-25 years) surrounded by pine (*Pinus patula*) plantation were selected from the Petrusvlei and Gilboa commercial forestry estates (hereafter: Gilboa fragments). Given the short generation times and potentially rapid turnover of epigaeic invertebrates and small mammals, it was assumed that a 12-25 year history of surrounding pine forest would give these communities enough time to be influenced by the matrix. A second set of five indigenous fragments was selected from the Balgowan region, which is a grassland dominated farming area (Fig 1). Mistbelt forests have been surrounded by grassland for at least 1000 years (Meadows and Linder, 1989) and it was assumed that the Balgowan fragments would contain a historically typical suite of mistbelt forest fauna with which to compare the Gilboa forest fauna.

In order to test the effect of reduction in forest area on epigaeic forest fauna, the selected forest fragments ranged in size from small (0.5 ha) to fairly large (215 ha). Each of the five fragments in the pine dominated Gilboa area was matched with a fragment of approximately similar size in the grassland dominated Balgowan area (Table 1). In cases where a substantial discrepancy exists between paired forest sizes (Table 1), forests were matched as closely as possible by area, given the limited number of forests in each of the selected complexes.

A much larger forest patch (705 ha) situated on the Leopards Bush Private Nature Reserve (Hereafter: Leopards Bush) (Fig 1), was sampled as a natural control for the effect of area and fragmentation on the forest taxa. Forming part of the continuous indigenous Karkloof forest range, this forest is relatively unfragmented (Fig 1). Extensive logging took place in the Karkloof forest prior to 1944 (Rycroft, 1944), however this activity was widespread among the forests of the region. Obviously logged-over forests were avoided in this study.

Table 1. Selected forest fragments showing forest area (ha) and landowners/managers. "Large forests (> 30 ha) in bold.

Balgowan (Grassland Matrix)	Area (ha)	Landowner/ Manager	Gilboa (Pine matrix)	Area (ha)	Landowner/ manager
BE	0.5	Sinclair	GE	0.5	Sappi
BD	3	Griffin	GD	1.7	Sappi
BC	15	MacKenzie	GC	13	Sappi
BB	**85**	**Griffin**	**GB**	**37**	**Mondi**
BA	**215**	**Kimber/ Sinclair**	**GA**	**105**	**Geekie**

2.2. Sampling methods

Epigaeic invertebrate communities were sampled in each of the selected forests along gradient oriented transects (GRADSECTS: Gillison and Brewer, 1985; Oliver and Beattie, 1996a), running from the edge of the fragments (0 m) into the interior, and up the slope where possible. Edge to interior and altitudinal gradients were perceived as the most obvious environmental gradients within the mistbelt forests. These gradsects were assumed to cover more micro-habitats than any other perceived gradients, and therefore sample a maximum representative invertebrate fauna in each forest given time and logistic constraints.

The forest patches were classified into "large" (> 30 ha) and "small" (< 30 ha) patches. Six epigaeic invertebrate trapping grids (quadrats) were placed along one gradsect in the large forests, and three quadrats were placed in the small forests. In the control forest, Leopards Bush, three gradsects at least 200 m apart, each containing six quadrats were used.

Each 3 m x 3 m quadrat, spaced at 20 m intervals, comprised 16 pitfall-traps each 1m apart (a trap was placed at each corner of the quadrat). Pitfall-traps were glass test tubes 150 mm deep, with a diameter of 25 mm. Each test tube was buried flush with the soil surface and contained 20 ml of alcohol and glycol in a 4:1 ratio.

Epigaeic invertebrates were trapped for 21 consecutive days between December 1997 and February 1998 in each forest in order to limit the effect of seasonality on population fluctuations. Samples were collected once a week when pitfall traps were reset. If there was heavy rain between servicing dates, traps were revisited and reset. Weekly samples were heat-sealed in plastic for storage and transportation. The invertebrates from each sample were sorted into morphospecies (Oliver and Beattie, 1996b) and where possible, specialists identified taxa to family level or lower.

2.3. Analyses

2.3.1. Measuring community similarity and cluster analyses

There are approximately two-dozen techniques used to measure similarity between communities (Legendre and Legendre, 1983; Wolda, 1981; Sneath and Sokal, 1973). Due to their descriptive nature, it is difficult to obtain reliable confidence intervals for most similarity measures. Errors can only be estimated using some type of randomisation procedure (Ricklefs and Lau, 1980). It is desirable for any similarity measure to (i) be independent of sample size and the number of species in the community, and (ii) increase smoothly from some fixed minimum to a fixed maximum as the two community samples become more similar (Wolda, 1981).

The Bray-Curtis dissimilarity coefficient (Bray and Curtis, 1957) has been shown to provide a robust estimate of the dissimilarity in structure between communities (Faith et al., 1987). It is most sensitive to differences in relative abundances between communities, although it is also affected by species richness and composition (Davies et al., 2001). As two communities diverge in terms of species abundance, the Bray-Curtis distance between the plotted communities increases from zero (similar communities) to one (dissimilar communities) (Krebs, 1989).

Cluster analyses allow ecologists to group communities based on their similarity coefficients, and are good tools to use when a number of communities are being compared. The group-average linkage clustering technique, used in this study to classify the communities, is a hierarchical, agglomerative cluster analysis, and is a modification of both the single and complete linkage clustering techniques (Krebs, 1989). Single linkage clustering tends to produce long, strung-out clusters whereas complete linkage clustering produces very tight, compact clusters (Krebs, 1989). Average linkage clustering produces intermediate results (Krebs, 1990). These analyses were made using PRIMER v4.0 (Clarke and Warwick, 1994). Data were fourth-root transformed prior to analysis to give equal weighting to rare and common species.

In addition, paired complementarity calculations (Colwell and Coddington, 1994) were used to assess biotic distinctness between forest fragments. Complementarity values range between 100% (no species shared) and 0% (identical species presence).

2.3.2. Nested subset analyses

Nested subset analyses are used to test whether there is convergence in species composition of a nested series of assemblages or communities. The epigaeic invertebrate data were tabulated in a species presence-absence matrix, with species ranked by number of occurrences and sites ranked by species richness.

The "Temperature Calculator" of Atmar and Patterson (1993) is suited to explore various features of nestedness. Other metrics (Patterson & Atmar 1986, Cutler, 1991, Simberloff and Martin, 1991; Wright and Reeves, 1992; Lomolino, 1996) measure nestedness in relation to the distribution of each species. These partial scores are then summed over species to compile community-wide patterns (i.e., counting "up" in a site x species matrix, then summing across columns). Each ordering of rows (=sites) produces a potentially different distribution of "holes" and "outliers" and a different nestedness score. In contrast, "temperature", T, assesses degrees of nestedness simultaneously across species and sites (i.e., counting diagonally across the matrix). Just as the species compositions of fragments can be nested within one another, so too can the incidence distributions of species. Neither deserves logical precedence in ecological analyses (Patterson and Atmar, 2000). Moreover, there is only one arrangement of "presences" in a distribution matrix that maximizes nestedness across both these dimensions. This essential structure can then be compared to numerous possible correlates without matrix reorganization.

Atmar and Patterson's (1993) 'temperature' metric was used for nestedness analyses. This method has the advantage over Cutlers' (1991) "U" metric of not being dependent on matrix size, and ranges from 0° for a perfectly nested matrix to 100° for one that is completely disordered (Wright et al. 1998).

Atmar and Pattersons "T" metric was calculated for the epigaeic invertebrate communities of each complex as a whole, and then for selected taxa (ants, beetles, flies, bugs,spiders, and combined predators) separately. Predators were selected as the top end of the food chain is usually more prone to extinction than species at lower levels because the former tend to have more unstable population dynamics and are less likely to persist in a fluctuating environment (Pimm and Lawton, 1977; Lawton, 1995; Holt, 1996).

2.3.3. Idiosyncratic species

Two forms of noise contribute to the temperature of a matrix (Patterson and Atmar, 2000): (1) the random variation of environmental, demographic, and genetic stochasticity; and (2) the "coherent" noise of specific biogeographic events or of ecologically distinctive species. Random noise creates a gray band of mixed presences and absences along the entire length of the boundary line. In contrast, coherent noise creates idiosyncratic "spikes" that correspond to species or islands that contribute much more noise than the remainder. Where temperatures are not uniformly distributed across islands and species, contrasting biogeographic histories or current ecologies are implied for those islands and species, respectively, than those that characterize the system as a whole (Patterson and Atmar, 2000).

2.3.4. The role of isolation and area in shaping invertebrate composition in Afromontane forest

If patterns are nested by non-random mechanisms it is possible to test whether the pattern is more likely to have resulted from selective extinction or colonisation (Lomilono, 1996). The Lomolino model assumes, from MacArthur and Wilson's (1967) theory of island biogeography, that the probability of immigration decreases with increasing isolation and that the probability of extinction decreases with increasing island size. Two presence-absence matrices of the epigaeic invertebrate data for the forest fragments were independently sorted by increasing isolation and then by area for each complex. Isolation was estimated by measuring the distance to the nearest forest fragment of equal or greater size. The deviations from perfect nestedness were then calculated by scanning down each ordered matrix and counting the number of times the absence of a species was followed by its presence in the next (smaller/more isolated) fragment. This index (D) is sensitive to variation in fragment sequence and gives equal weight to presences and absences of species (Lomolino, 1996) which Patterson and Atmar's (1986) N index does not do (Atmar and Patterson, 1993). Statistical significance of nestedness was estimated for each matrix by comparing the D values to values (R) obtained for matrices in which species distributions remained the same while island sequence was randomly ordered with respect to isolation and area (Lomolino, 1996). This analysis was performed using the program NESTSEND (Lomolino, 1996).

3. Results

3.1. Cluster analyses

All forests were at least 70 % similar in community composition (Fig. 2). Smaller forests (< 30 ha) tended to be more similar to each other than to larger forests regardless of surrounding matrix type suggesting a pervasive edge effect in small fragments (with the exception of Gilboa "A" and Balgowan "E"). The larger Balgowan (> 30 ha) forests situated within a "natural" grassland matrix were grouped with Karkloof (control forest) while the two large Gilboa fragments were not (Fig. 2).

The complementarity analysis indicated fairly low biotic distinctness over all forests, with only one pair of forests having over 50% of species unique to one of the pair (cf. Kotze et al., 2000), two of which include Gilboa "C" (Table 2). This forest is the most heterogenous in terms of leaf-litter cover (Chapter 4), an important habitat variable for epigaeic invertebrates, and this heterogeneity may influence species composition. In other words, all the forest pairs compared (with three exceptions), share at least 50% of their species, regardless of forest area or matrix type. There were 37 species (22%) common to all forests sampled.
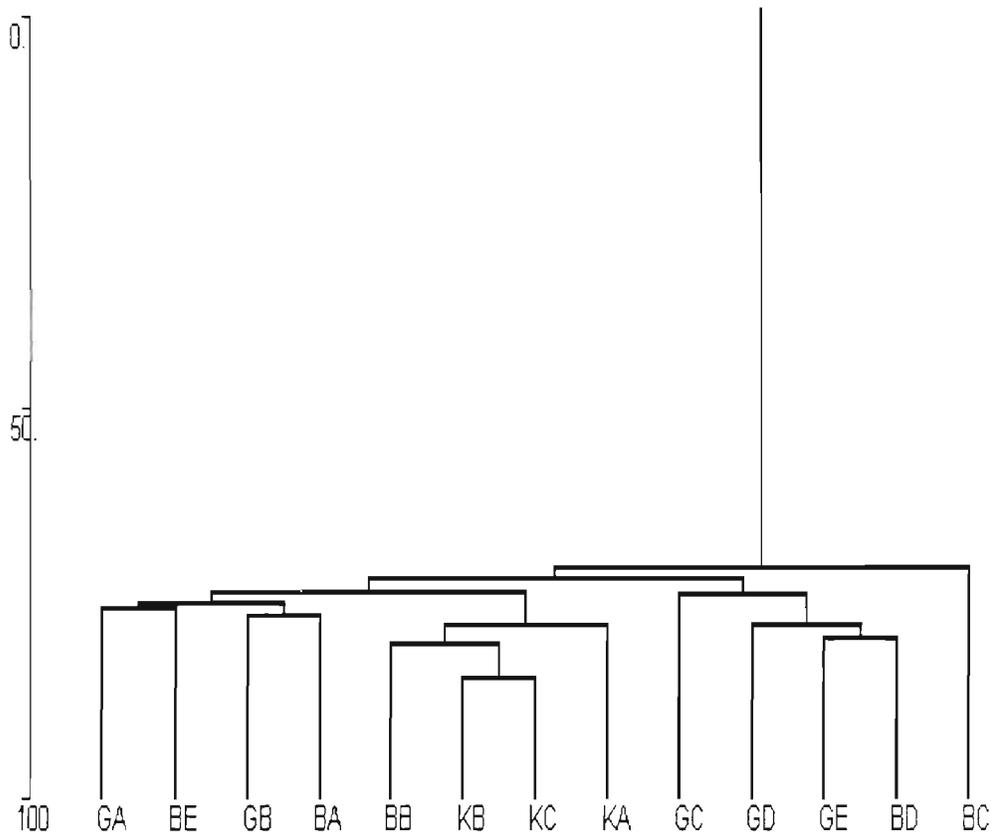
Fig. 2. Dendrogram showing similarity of forests to each other; using a Bray-Curtis similarity measure and group average linkage. Vertical axis represents percentage similarity; Horizontal axis represents forests (see table 1 for explanation of acronyms).

Table 2. Complementarity percentage between forests. Values in parentheses after forest names are the total number of epigaeic invertebrate species captured in that forest. Values in parentheses after complementarity percentages are the number of epigaeic invertebrate species shared between the two forests compared.

	PA (99)	PB (107)	PC (74)	PD (73)	PE (73)	BA (113)	BB (95)	BC (85)	BD (79)	BE (80)
PB (107)	39 (78)	--								
PC (74)	47 (60)	49 (61)	--							
PD (73)	45 (61)	41 (67)	40 (55)	--						
PE (73)	44 (62)	45 (64)	40 (55)	34 (58)	--					
BA (113)	39 (80)	36 (86)	47 (65)	45 (66)	46 (65)	--				
BB (95)	40 (73)	41 (75)	36 (66)	42 (62)	34 (67)	40 (78)	--			
BC (85)	45 (65)	41 (71)	51 (52)	44 (57)	42 (58)	43 (72)	47 (62)	--		
BD (79)	40 (67)	44 (67)	47 (53)	37 (59)	33 (61)	43 (70)	40 (65)	41 (61)	--	
BE (80)	39 (68)	43 (68)	48 (53)	44 (55)	41 (57)	38 (74)	38 (67)	44 (59)	36 (62)	--
K (127)	39 (86)	38 (90)	53 (64)	51 (66)	47 (69)	36 (94)	34 (88)	43 (77)	49 (70)	44 (74)

3.2. Nested subset analyses

Neither Balgowan nor Gilboa epigaeic invertebrate communities were significantly nested as both observed "temperatures" fell within the range predicted (i.e. observed "temperatures" did not differ significantly from those randomly generated) by the temperature calculator programme (Atmar and Patterson 1993). However, in both cases the average temperature produced by the Monte-Carlo simulations were hotter than those observed, indicating a tendency towards nestedness. The Balgowan flies and the Gilboa bugs were the only orders to produce significantly "colder" observed than expected matrices (significantly nested) (Table 3). In addition, the predators did not exhibit nestedness but also tended towards nestedness. There were 48 idiosyncratic species (i.e. those species causing "hotter" temperatures) among the Balgowan epigaeic invertebrates while 38 were found in the Gilboa invertebrates.

Table 3. Results of matrix temperature calculator (Atmar and Patterson 1993). Bold rows represent significantly cooler (more nested) matrices (Tm) than those generated randomly (Te).

Complex	Species	Taxon	Matrix Temperature (Tm)	Expected Temperature (Te ± SD)	Fill	Idiosyncratic species	p
Balgowan (n = 5 Islands)	142	All	42.6	47 ± 4.8	45.6	48	0.17
	10	Ants	35.4	33.4 ± 12.6	55	4	0.5
	51	Beetles	37.9	43.5 ± 6.7	45.5	19	0.2
	8	Bugs	10.2	24.2 ± 16.35	60	2	0.2
	20	**Flies**	**32.6**	**30.6 ± 12.3**	**35.5**	**3**	**0.05**
	19	Spiders	30.5	36 ± 10.5	45	4	0.3
	42	Predators	34.9	40.1 ± 7.9	46.1	10	0.22
Gilboa (n = 5 islands)	140	All	40.9	47 ± 4.9	41.6	38	0.1
	12	Ants	29.6	36.4 ± 10.7	48.3	6	0.26
	39	Beetles	41.8	46.9 ± 8.9	50	10	0.28
	9	**Bugs**	**13.1**	**33.4 ± 12.6**	**52.5**	**3**	**0.05**
	22	Flies	16	32.4 ± 11.1	35	4	0.07
	20	Spiders	28.9	36.4 ± 9.4	45	6	0.2
	45	Predators	32.8	42.6 ± 7.7	45.1	11	0.1

3.3. Epigaeic invertebrate community structure: shaped by extinction or colonisation processes?

The Lomolino model showed no significance of nestedness when sites were ordered by either area or isolation with the exception of the Gilboa fly community that was significant (P < 0.05) when sites were ordered by area (Table 4). However, archipelagos ordered by area tended to have lower probability values than those ordered by isolation (Table 4).

Table 4. Results of analysis of nestedness, with forests ordered by isolation and area
(Lomolino 1996) for epigaeic invertebrates (significant values highlighted). "P" is the
probability value for the statistic.

Complex	Invertebrate group	Area (P=)	Isolation (P=)
Balgowan	All invertebrates	0.085	0.71
Gilboa	All invertebrates	0.125	0.979
	Ants	0.882	0.882
	Beetles	0.237	0.074
Balgowan	Bugs	0.267	0.267
	Flies	0.376	0.376
	Spiders	0.711	0.916
	Ants	0.124	1
	Beetles	0.154	0.154
Gilboa	Bugs	0.356	0.181
	Flies	**0.035**	0.155
	Spiders	0.556	0.556

4. Discussion

4.1. Cluster analyses

Where community structure and composition is driven by deterministic extinction effects and are therefore significantly nested within an archipelago, there will be convergence of species composition as habitat fragments become smaller. This process occurs as follows: an area of suitable habitat, initially inhabited by a common ancestral biota, is fragmented into an archipelago of islands by climatic change (Patterson and Atmar, 1986). On each island of an archipelago, there will be one species that is nearest its minimum viable population size, and thus at greatest risk of local extinction. As area continues to shrink, populations of the archipelagos constituent species will tend to go extinct in order of their various extinction risks (Atmar and Patterson, 1993), such that small islands reach a common species pool. The cluster dendrograms show that epigaeic invertebrates in this study conform to this trend, with the communities in the small forests grouping together regardless of matrix type. Large forest communities were grouped separately from those in the smaller forests, and those in a pine matrix were separated from those in a grassland matrix. This suggests that matrix type had an effect on large forest (i.e. over 30 ha) epigaeic invertebrate communities. However, forest communities were very similar and shared 22% of all invertebrate species recorded resulting in low complementarity values. These common invertebrates consisted of generalist feeders; 14 predators (1 ant, 7 beetles, 5 spiders and 1 centipede), 13 decomposers (10 flies; larval phase, one amphipod, 1 millipede, 1 isopod); three phytophages (2 beetles, 1 cricket), two

saprophages (bugs), one omnivore (cockroach) and four unidentified species. The large number of shared generalist species suggests that extinction prone species had already become extinct in these forests, giving way to more vagile, generalist or eurytopic species.

4.2. The nested subsets phenomenon in mistbelt mixed Podocarpus forest fragments

The primary biological significance of dispersal is to maintain and extend the presence of a species in space by (re)founding and supplementing local populations (Den Boer, 1990). Invertebrates are very successful colonisers (Den Boer, 1990), even over inhospitable habitats such as agricultural land (Duelli, 1990) and oceans (Crawford et al., 1995, Den Boer, 1990; Peck, 1990, 1994; Rey and Strong, 1983). Extinction rates may be high and persistence low in the early stages of colonisation (Hahn and Tschinkel, 1997; Rey and Strong, 1983), with persistence depending on habitat suitability (Turner, 1992). However, while many arthropods exhibit remarkable powers of dispersal and colonisation, barriers as seemingly insignificant as paved agricultural roads or hedgerows may hamper dispersal, especially in the case of ground-foraging dispersers such as certain beetles, and spiders (Mader et al., 1990; Mauremooto et al., 1995). Studies have shown that even some avian species are excluded from indigenous habitat that is surrounded by coniferous forest (e.g. Estades and Temple, 1999).

The mistbelt-mixed Podocarpus forests have been fragmented for a long time (Lawes, 1990; Eeley et al., 1999), forming an archipelago of isolated habitat "islands" (forest fragments), that share a common regional species source. This is an important assumption when dealing with communities whose structure is determined by colonisation and/or extinction events (Cutler, 1991; 1994).

The results of this study indicate that epigaeic invertebrate communities in these forest complexes are not nested, and that all forests are fairly similar in terms of species composition, sharing 22% of their species. These results are counter-intuitive, as some degree of nestedness appears to be the rule in nature (Wright et al, 1998). However, Wright et al. (1998), found that there were a few archipelagos out of the 279 analysed in which the communities under study were significantly non-nested i.e. had species communities that were more heterogenous than expected by chance. In most cases these data were from experiments on the effects of immigration or extinction on coastal arthropod communities. Nine out of ten archipelagos that rated as anti-nested were from arthropod experiments (Simberloff and Wilson ,1969; Rey, 1981). Simberloff and Wilson (1969) found similar results to those in this study in a series of six mangrove islands in southern Florida. In a pre-treatment (defaunation) census of these islands, 250 terrestrial invertebrate species were recorded. The species presences did not produce a nested series (Matrix fill = 32 %; T_m = 51.9; $T_e \pm SD$ = 50.8 ± 3.1; p ($T_m < T_e$) = 0.6). Following defaunation, immigration of invertebrates onto these mangrove islands still had not produced a significantly nested matrix after 57 weeks. In fact, the matrix was slightly less nested than before the defaunation (Matrix

fill = 31 % Tm = 53. 7; Te ± SD = 52.5 ± 3.8; p (Tm < Te) = 0.6), indicating that immigration alone did not lead to nestedness.

Although predators are thought to be more prone to extinction than species from lower trophic guilds, the findings of this study showed a non-nested guild structure. Again, this is counter-intuitive if these predators are from an extinction-prone guild. Davies *et al.* (2000) found that isolated beetle predators as a whole were no more vulnerable to extinction than herbivores or detritus feeders, although among those species that declined in response to fragmentation, predators declined most. It is probable that the species in this study are mostly generalist predators and are able to survive in fragmented conditions, as they made up the highest proportion of any guilds common to all forests (38 %).

Idiosyncratic species might variously recolonize some islands from which they have been locally extirpated, reach their range limits in the midst of the archipelago, or be victims of competitive exclusion or products of local speciation (Patterson and Atmar, 2000). The anti-nested nature of the epigaeic invertebrates in this study may have been due to invasion of the mistbelt mixed *Podocarpus* forest fragments from the matrices by generalist species, with higher numbers invading from the grassland matrix as a natural result of the higher numbers of invertebrate species found here. Variation around the extinction threshold boundary of the packed matrix produced by the temperature calculator programme (cf. Atmar and Patterson, 1993) for the epigaeic invertebrates in this study was high (less nested) compared to truly isolated species such as the terrestrial isopod and land snail communities of the Kyklades islands of Greece (Sfenthourakis *et al.*, 1999), which were highly significantly nested and extinction-driven.

4.3. The impact of isolation of mistbelt mixed Podocarpus *forest fragments on epigaeic invertebrate communities*

Isolation of forest fragments appears to have no influence in determining the invertebrate community compositions on these islands. This leaves the question of the correct measure of isolation open to some debate. Lomolino's approach to the causality of nestedness assumes that immigrations and extinctions are correlated with the ordering variables (isolation and area) (Lomolino, 1996). In addition, it assumes that area and isolation are uncorrelated and that immigrations are not correlated with island area (i.e. no target effect) and that extinctions are not correlated with isolation (no rescue effect; Brown and Kodric-Brown, 1977; Lomolino, 1986). While it is a simple matter to obtain a measure of island area, any measure of isolation must be biologically significant at the level of the organisms being studied and this is very difficult to do (Lomolino, 1996), especially with a group as diverse (i.e. with differing responses to external factors) as the epigaeic invertebrate community. It is highly likely, although not tested in this study, that pine plantations, which themselves support lower diversity than surrounding indigenous areas (Armstrong and van Hensbergen, 1994; Donnelly and Giliomee, 1985; Mboukou-Kimbatsa *et al.*, 1998;

Richardson and van Wilgen, 1986; Romero-Alcaraz and Avila, 2000), act as dispersal barriers to epigaeic invertebrates. Pine plantations characteristically show a lack of herb and grass cover, undeveloped under-storey layers, and a dense litter layer of pine-needles. Pine plantations simplify vegetation structure (York, 2001) and smother invertebrate species richness in many instances (Armstrong et al.,1998; Donnelly and Giliomee, 1985; Pryke, 1999; Romero-Alcaraz and Aliva 2000).

The question of how difficult it is for these animals to disperse through pine plantations compared to grassland remains unanswered. This study did not sample epigaeic invertebrates in the grassland and pine matrices to identify those species that have invaded the mistbelt forests, but this is a further research opportunity in this area.

Assuming an extinction-driven community structure of epigaeic invertebrates and due to the similarity of the communities throughout all forests, and the lack of nestedness observed, I expect that convergence of epigaeic invertebrate communities has already taken place in the smaller fragments, with patterns of convergence being clouded due to subsequent and ongoing invasions from the matrix. Larger forests still remain separated into their matrix types, and this could mean that the matrix is affecting species composition in them, a prediction supported by the density compensation findings results in chapter 4.

In the following chapter I investigate how individual species respond to the fragmentation and matrix transformation of the Karkloof/Balgowan/Gilboa forests, and attempt to identify ecological indicators of forest condition from the epigaeic invertebrate community.

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CHAPTER 4

The diversity and species-area relationships of epigaeic invertebrate assemblages in isolated mistbelt mixed *Podocarpus* forest fragments

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Abstract

The Afromontane region of South Africa is characterised by numerous small and few large remnant mistbelt-mixed *Podocarpus* forest fragments that are historically surrounded by an indigenous grassland matrix. During the past 100 years commercial forests (*Pinus* spp.) have replaced much of this native grassland. The pine (*Pinus patula*) matrix is inhospitable to most organisms using the litter layer, and affects their natural dispersal between habitat patches. Using pitfall traps I investigated epigaeic invertebrate community structure in two sets of five mistbelt forests; one in a pine matrix (Gilboa) and the other in a grassland matrix (Balgowan). The forests ranged in area from 0.5 ha to 215 ha. The species regression of the epigaeic invertebrate communities in the Gilboa forest complex was positive but not significant, with large residual values. Communities in the Balgowan forest fragments showed a significant species-area relationship and exhibited density compensation. The Gilboa invertebrates did not show density compensation. Predictions of species-area equilibrium may therefore hold for Balgowan but not for Gilboa. Edge effects appeared to penetrate deeper into the forests than was expected, and habitat diversity did not significantly affect the α diversity index or species richness in either complex.

Key words: commercial forestry; density compensation; diversity; epigaeic invertebrates; forest; fragmentation; island biogeography theory; matrix effects; pine; species area.

1. Introduction

The historically fragmented Afromontane mistbelt-mixed *Podocarpus* forests (Meadows and Linder, 1989; Lawes *et al.*, 1999) of the KwaZulu-Natal midlands pose a conservation and management dilemma for the survival of their constituent fauna. Logging activities in the past (mainly from 1860 to 1940) have altered forest habitat quality, while alteration of matrix habitats has resulted in the encroachment of agro-commercial activities (e.g., commercial plantation forestry) on the forest boundary (Macfarlane, 2000) and reduced the possibility of dispersal among patches. Fragmentation effects are ongoing and subtle, but are largely ignored.

Although the theoretical effects of habitat isolation and area reduction are well known for vertebrates (see Rosenzweig, 1995 for review), invertebrates have been overlooked in studies of area and isolation effects. It has been suggested that because invertebrates have small critical habitat area requirements, as well as high fecundity and short generation times, they are unlikely to be affected by all but very intensive fragmentation effects (e.g., habitat clearance) (Putman, 1994; Chapter 5) and are not useful indicators of environmental change

at a gross scale (resilience hypothesis; Heliovaara and Vaisanen, 1984). Others would argue that invertebrates are useful indicators precisely because they are small, hyperdiverse and highly sensitive to changes in their environment (Kotze and Samways, 1999). Indeed, short generation times may allow invertebrate populations to respond rapidly to any disturbances (response hypothesis; Putman, 1994). Some invertebrate groups may therefore be good indicators of habitat heterogeneity, ecosystem diversity and environmental stress (Dempster, 1991; Colwell and Coddington, 1994; Weaver, 1995; McGeoch, 1998). For example, Kotze and Samways (1999) found that significantly fewer species and individuals of four invertebrate taxa (ants, spiders and, carabid and staphylinid beetles) were captured in small forest patches (< 6 ha) compared to large forest patches in a grassland matrix.

Assemblage and community level responses of species to fragmentation have been largely investigated using species-area theory (Rosenzweig, 1995). Species-area theory is based upon the equilibrium theory of island biogeography (Preston, 1960; MacArthur and Wilson, 1963, 1967). However, this study does not examine the equilibrium theory *per se* because the predictions were not tested (see Gilbert 1980; Brown and Dinsmore, 1988). Nevertheless, the basic tenets of the equilibrium theory are assumed in much of the species-area analyses used. In its most basic form the species-area relationship is a monotonic increase in the number of species with increase in area for a set of sites (Williams, 1964; Connor and McCoy, 1979; Simberloff, 1992). This relationship is explained as the outcome of local extinction of species already on the island and the immigration of species from source areas to the island (Simberloff, 1992). In general, larger islands contain more species because they have larger populations that are less vulnerable to deterministic (e.g., area dependent) or stochastic (e.g., disease, climatic catastrophe) extinction effects (Pielou, 1977; Dennis *et al.*, 1991).

In the absence of tests of the predictions of the equilibrium theory of island biogeography in this thesis (e.g. testing for dynamic turnover of species at equilibrium), species-area analyses should be used cautiously, if only because a positive species-area relationship alone may not represent an equilibrium state. In order to test for an equilibrium state, five falsifiable predictions must be tested (Brown *et al.*, 1995). In this study, only one of the five, a positive correlation between species and area, was tested. The assumption of stable species equilibrium in the use of species-area theory has been questioned on two further points. First, in natural systems the environment is continually changing, often with pronounced effects on populations (Chesson and Case, 1986), and species assemblages are unlikely to achieve a stable equilibrium. Secondly, the species in many communities do not appear to have many of the attributes necessary (e.g., ability to survive changing conditions and perturbations) for stable species equilibria (Chesson and Case, 1986). Epigaeic invertebrates may be among the few taxa that do possess these attributes due to their rapid turnover rates and their ability to survive changing environmental states *in situ.*

A further consideration of the application of species-area theory to conservation of insular faunas, and the explanation of the common species-area effect, is the influence of

habitat diversity. Williams (1964) argued that as the area sampled increases so do the number of habitats with their associated species, and thus number of species increases with area but as a function of increasing habitat diversity.

The influence of isolation of habitat fragments on epigaeic invertebrate species assemblages warrants brief mention as fragmentation and isolation of habitats go hand in hand. Animals that are able to disperse will colonise areas along dispersal routes in a predictable manner due to differential immigration ability (Cutler, 1994), with more isolated fragments being populated by a subset of more mobile species.

However, most leaf-litter invertebrates (i.e. epigaeic invertebrates) are unable to move away from and out-distance local disturbances because many species rely entirely upon the resources provided by the organic leaf-litter layer (Hammond, 1990; Holloway and Stork, 1991). Consequently, epigaeic invertebrates have to respond to pressure effects *in situ*, and a wider spectrum of species may show a common response to, and reflect current conditions within, the habitat. Thus isolation may be of less importance than area reduction in the shaping of epigaeic invertebrate species assemblage in this instance and is discussed in Chapter 3.

Density compensation usually describes an inverse relationship between population density and species richness (McGrady-Steed and Morin, 2000; Stevens and Willig, 2000). However since species richness is a positive function of area, if we assume that the density of a group of species is constant per unit area, then the individual species must, on average, decrease in larger areas (Schoener, 1986). Density compensation may thus be a natural corollary of density-area effects. This relationship is investigated in the Balgowan and Gilboa complexes.

Epigaeic invertebrates comprise the majority of fauna in forests and fill a wide variety of functional roles necessary for the functioning of these ecosystems (Samways, 1994). Pitfall trapping estimates the relative population levels of mobile epigaeic invertebrates, and thereby measures their relative importance on the forest floor (Greenslade, 1964, 1973; Greenslade and Greenslade, 1971; Majer, 1978). Taking into account the matrix (grassland or commercial plantation) surrounding forests, and by using a representative sample (area and isolation) of forest fragments within each matrix type, I investigated the effects of fragmentation on epigaeic invertebrate diversity in Afromontane mist-belt forest by targeting epigaeic invertebrates as a group, and then looking more closely at five taxa (beetles, flies, ants, spiders and bugs). I assessed their responses, if any, to changes in forest area, matrix type and habitat heterogeneity. Species-area theory was used to test whether invertebrates were responding to gross fragmentation effects. If a positive species-area relationship were found, this would indicate that epigaeic invertebrate communities were responsive to habitat reduction, but not necessarily in equilibrium. If a positive species-area curve were not found, then the communities would not be in equilibrium.

2. Method

2.1. Study site and selection of forest fragments

See Chapter 3, section 2.1.

2.2. Sampling methods

See Chapter 3, section 2.2

2.3. Problems associated with sampling habitat islands of unequal area

Large habitats may receive effectively more samples than smaller habitats, and greater species richness in large patches may reflect the greater number of samples. This is termed the "sampling effect" (Hill et al., 1994). The sampling effect is based on the assumption that all individuals in a community are located at random and therefore the chance of finding any particular species is simply a function of the total area sampled and the number of individuals in the community (Hill et al., 1994). Although species actually show a non-random distribution, the sampling effect still exists and must be removed from the data before ecological factors can be invoked to describe species richness trends (Hill et al., 1994). Large habitat fragments may be more obvious targets and therefore be sampled more heavily than small (i.e. less conspicuous) fragments (Stevens, 1986; Rosenzweig, 1992). Conversely, when both large and small habitat islands are sampled, relative to their area, large habitats are often not sampled as intensively as smaller islands. Rarefaction of abundance data collected in habitats of unequal area corrects for these sampling inconsistencies and permits species richness comparisons across patches or islands of differing areas (James and Rathburn, 1981; Simberloff, 1972).

Due to habitat heterogeneity, the diversity of any quadrat is less than that of the community from which it is sampled. Zahl (1977) proposed the Jackknife procedure to address the problem of estimating species richness from quadrat samples. Heltshe and Forrester (1983) advocate this procedure above Pielou's (1966) pooling procedure for estimating diversity from quadrat sampling.

2.3.1. Jackknife and rarefaction techniques

The Jackknife 1 procedure was used to estimate what proportion of the total species were sampled in each forest (Colwell and Coddington, 1994). The rarefaction method (Krebs, 1989) assumes that the number of individuals present represents a random sample from the pool of all individuals and species available (McGuinness, 1984), and reduces all samples to

a common number of individuals (Simberloff, 1972; James and Rathburn, 1981; Magurran, 1988; Duelli *et al.*, 1999). Species richness is estimated for that common number of individuals in each habitat island, allowing direct comparison of standardised species richness for all samples.

2.4. Vegetation analysis

The floristics, physiognomy, and selected environmental variables were measured in the eleven forest fragments in 10 m x 10 m quadrats that were coincident with the pitfall quadrats along each gradsect in each forest. Vegetation variables and epigaeic invertebrates were thus sampled over the same spatial scale and at the scale of response of the invertebrates to environmental and habitat quality.

All trees with a diameter at breast height (DBH) > 10 cm, and saplings (1 cm < DBH < 10 cm) within a quadrat were identified to species level. The DBH was measured and height was estimated. Since multi-stemmed trees are often an indication of disturbance (Midgley and Cowling, 1993; Bellingham *et al.*, 1994; Stearns, 1994; Kruger *et al.*, 1997; Holness 1998), multi-stemmed trees were identified and counted, along with the number of stems and the estimated medial DBH for each multi-stemmed tree. Canopy cover was measured at five random points in each quadrat using a moose-horn (Stromberg, 1995), and mean percentage canopy cover was calculated for each quadrat. Canopy cover was measured because dense upper-story vegetation shades understory vegetation and can influence soil moisture content (Samways *et al.*, 1996). For instance, soil under *Acacia mearnsii* becomes desiccated more quickly than soil under grass (Versveld and van Wilgen, 1986). This has consequences for species less resistant to desiccation. Each 10 m × 10 m quadrat contained three randomly positioned 1 m × 1 m sub-plots. Within each of these sub-plots, mean herb or grass height and cover was estimated visually.

Many of the invertebrates collected using the pitfall method rely entirely upon the organic leaf-litter layer for resources (Hammond, 1990; Holloway and Stork, 1991). The leaf-litter depth was measured using a steel rod 4 mm in diameter inserted into the leaf-litter until the harder soil layer was encountered. Mean depth was estimated from five measures in each sub-quadrat. The percent leaf-litter cover was visually estimated in each of the three 1 m^2 quadrats.

2.5. Estimating abundance and measuring diversity

In assessing species responses to environmental change it is not sufficient to look only at species richness. The species richness of a community is only altered when species are removed through extinction without replacement, or added through colonization without the corresponding loss of another species. Most species responses to changes in the environment are not as drastic as extinction of the entire population, but rather an increase or

decrease of abundance (Olson and Andriamiadana, 1996). Species diversity is the combined measure of the number of species in a community (or species richness) and the relative abundance of those species (Peet, 1974). I therefore used a suite of diversity indices in this study to assess species responses to environmental change at a finer scale than species richness in itself provided. Epigaeic invertebrate species richness, abundance, diversity and evenness indices (see below) were calculated using PRIMER (Clarke and Warwick, 1994) for all forests sampled.

i.   Alpha diversity index (α index) (Krebs, 1989)

ii.   Pielou's evenness index (J' or E1 = H'/ln [S]) (Pielou, 1975; 1977)

iii.   Shannon-Weiner diversity index (H') (Krebs, 1989)

iv.   Hill's number (N1 = Exp[H']) (Hill, 1973)

v.   Hill's number (N2 = 1/Si) (Hill, 1973)

vi.   Simpson's dominance index (SI = sum (Pi^2)) (Simpson, 1949)

vii.   Whittaker's β diversity (βw = (S/α) - 1) (Whittaker, 1960)

where S = the total species richness of each forest, and α = the total species richness for each quadrat.

Invertebrate community structure was compared between complexes as a whole and Leopards Bush, within each forest complex and Leopards Bush, and between complexes by area-paired forests. Comparisons were made using one-way anovas in MINITAB release 13.1. I favored the use of the alpha diversity index (hereafter α-index) because it is more stable than the Shannon-Weiner function under conditions of increasing sample size (Magurran, 1988), and is less affected by abundance of the most common species (Taylor *et al.*, 1976). The log-series variable - alpha - is commonly used as a diversity index, especially for entomological data. It assumes that the sample is a reasonable fit to a log-series and this is often the case and alpha appears to be robust (Fisher *et al.*, 1943; Kempton and Taylor, 1974). The α index is simple to calculate and interpret (Magurran, 1988). It is low when diversity is low, and high when diversity is high (Krebs, 1989). In addition, the large number of investigations into the behaviour of α and its satisfactory performance in a wide range of circumstances make it a good universal diversity statistic (Southwood, 1978). The Shannon-Wiener function (H') was however calculated for computation of the Hill's number (N1) and Pielou's evenness index (J) (Krebs, 1989). Epigaeic invertebrate point diversity (α diversity, or species richness per quadrat), and differentiation diversity (β diversity, or species turnover between quadrats and forests) were calculated (Magurran, 1988). β diversity is essentially a measure of how different (or similar) a range of habitats or samples are in terms of variety (and sometimes the abundances) of species found in them (Magurran, 1988). Whittaker's measure of β diversity (Whittaker, 1960) was used to measure species turnover between quadrats within the forests (Magurran, 1988; Kotze and Samways, 1999; Magura *et al.*,

2001). A minimum measure (0) represents no species turnover, and this value increases as turnover does (Magurran, 1988).

2.6. Species-area analysis

Least-squares linear regressions of log-species on log-area for the two complexes were plotted and compared for accuracy of fit to untransformed and semi-log plots. Species-area regressions based on untransformed data fitted best. The island effect or slope for complexes in different habitat matrices was thus compared. Least-squares linear regressions were performed using routines in STATGRAPHICS version 7 (Manugistics, 1993).

2.7. Habitat heterogeneity

Habitat heterogeneity refers to the number of different habitats encountered in any one forest. Williams (1964) suggests that the species-area relationship derives largely from a correlation between area and habitat diversity. As area increases, the number of habitats, each with an associated set of species, also increases. I used a statistical estimate of habitat heterogeneity in lieu of a direct measure of general habitat heterogeneity. The standard deviations of thirteen environmental variables for each forest were entered into a principal components analysis (PCA) as the standard deviations provided a measure of environmental variability. The first component derived from the PCA was used as an indirect measure of habitat heterogeneity.

3. Results

A total of 61 282 epigaeic invertebrates, representing 168 morphospecies (Appendix 1-3) were collected. Amphipods, molluscs, millipedes, beetles, wasps, ants, and flies were identified by specialists to family or genus and species level where possible (Appenidx 4), confirming the morphospecies. The single amphipod species, *Talistroides africana*, dominated the samples in
both Gilboa (37% of individuals; Fig 1) and Balgowan (32%; Fig 1). *Tetramorium sp.* (probably *T. avium*) (Hymenoptera: Formicidae) comprised 15% and 10% of individuals, and Staphylinidae *sp.* 1 6.5% and 7% of the total abundance of invertebrates in the Gilboa and Balgowan forests respectively. In the large (control) Karkloof forest the abundance of the four dominant species was more evenly distributed than in the two forest complexes (Fig 1). Amphipods (*Talistroides africana*) made up 13.5%, followed by *Tetramorium avium* (12.7%), *Sphaeroceridae sp. 2* (Diptera) (11.9%) and *Staphylinidae sp. 4.* (Coleoptera) (11.1%).
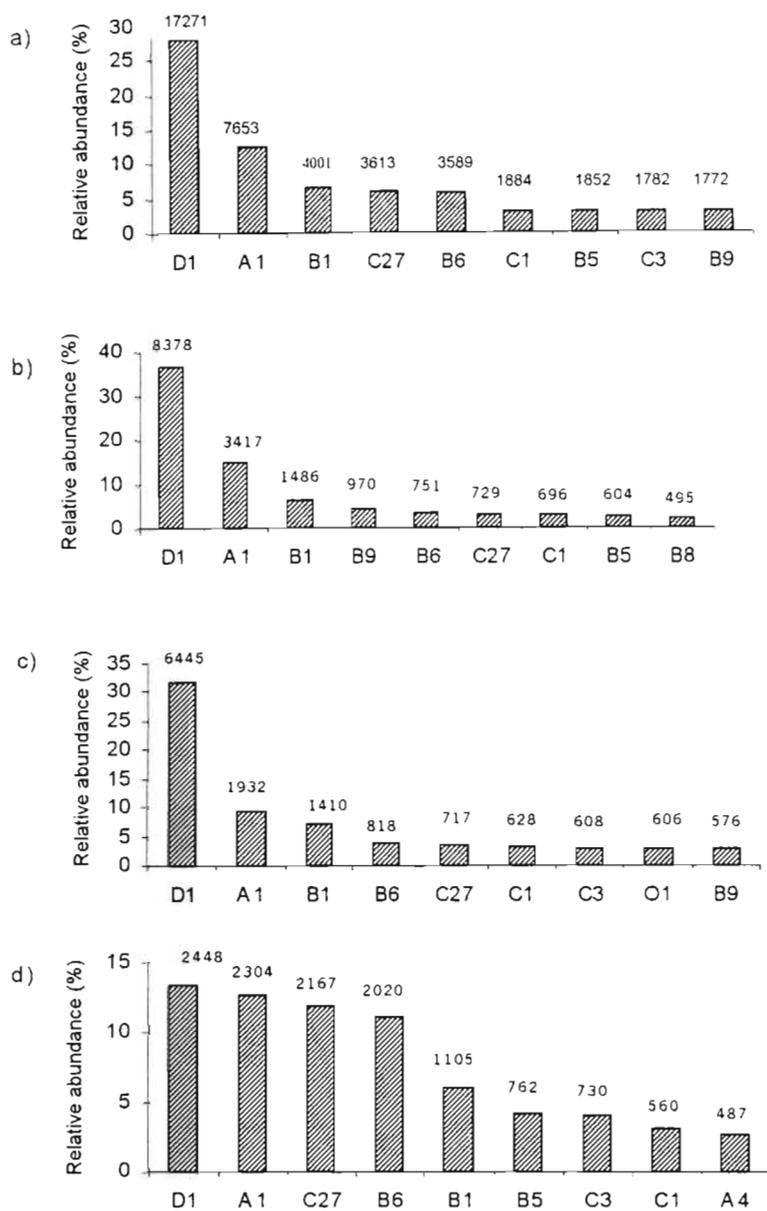
Fig. 1. (a) Relative abundance of the most dominant invertebrate species (comprising > 2% of the total) at all sites, (b) Gilboa, (c) Balgowan, (d) and Leopards Bush - Karkloof. Values above bars represent numbers of individuals, and x-axis categories refer to individual morphospecies.

Sampling saturation was not achieved in any of the sampled forest fragments; species accumulation curves showed decreasing accrual with increasing sampling, but were still increasing slowly when sampling ceased (Fig. 2 a, b, c). However, this was expected; in groups such as tropical arthropods observed richness rarely reaches an asymptote, despite intensive sampling (Gotelli and Colwell, 2001).
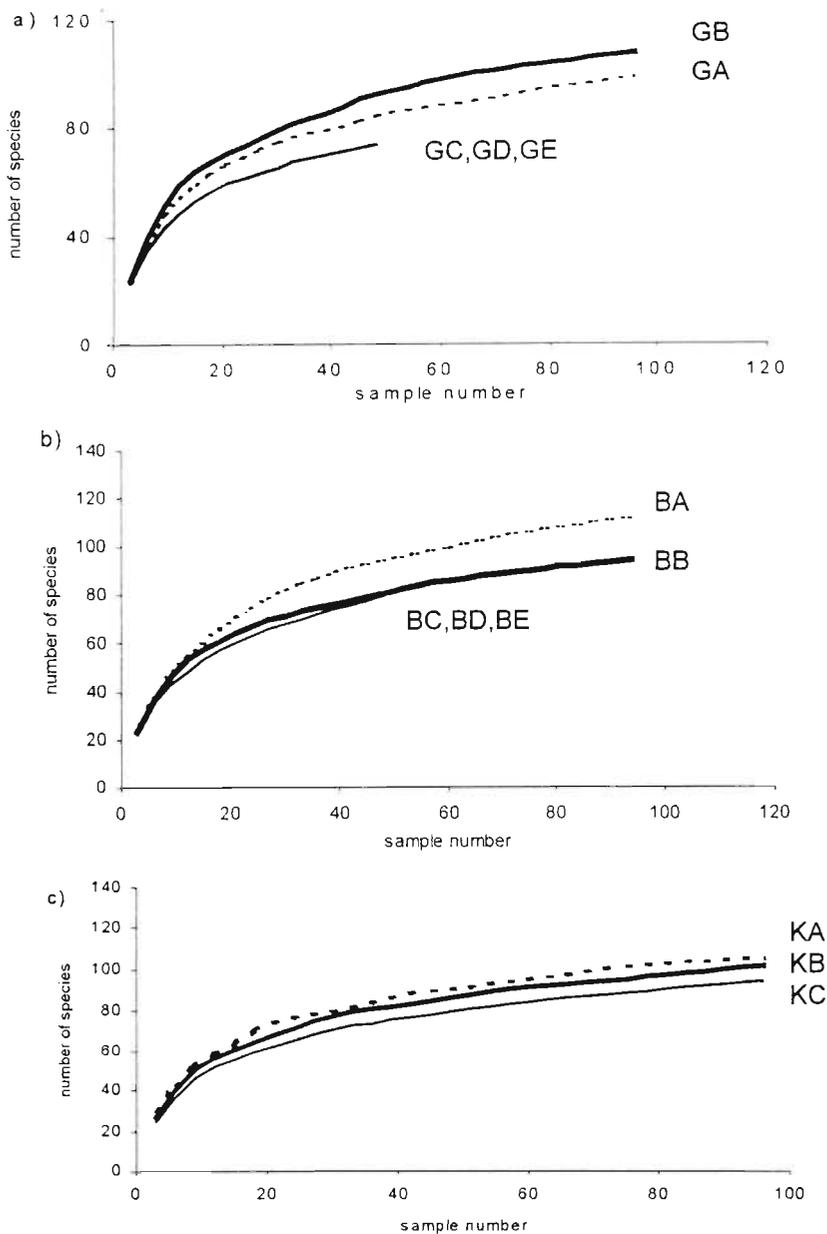
Fig. 2. Cumulative curves for epigaeic invertebrates collected at (a) Gilboa , (b) Balgowan and (c) Karkloof.

Using the Jackknife 1 procedure I calculated that on average 83% of the total number of species potentially present in the Gilboa complex were sampled. In the Balgowan complex this figure was estimated at 82 %. A higher estimated proportion of the species pool was recorded from the larger Balgowan forests, indicating that sampling efforts were adequate, or

at least similar to those in the smaller forests. The Gilboa complex and Karkloof forest yielded an estimated 83% and 84 % of the potential species pool of epigaeic invertebrates.

3.1. Rarefaction

Standardized species richness values were estimated from 2 311 individuals (the least abundant biota) per forest. In other words, all species richness estimates were obtained from a standard sample of 2 311 individuals, the lowest number of individuals obtained from any forest. The Balgowan complex exhibited a highly correlated, significant positive increase in alpha diversity with increasing area (Fig. 3; Slope =0.05; R^2 = 92%; $F_{1,3}$ = 36.5, p = 0.01; df = 4). The Gilboa forests showed a species-area trend that appeared positive, but the slope was in fact not significantly different from zero (Fig. 3; Slope = 0.015; R^2 = 19%; $F_{1,3}$ = 0.68 p = 0.47; df = 4)., indicating low diversity in the larger pine-surrounded forests compared with (i) the smaller forests in the same complex and (ii) the large forests within a grassland matrix.
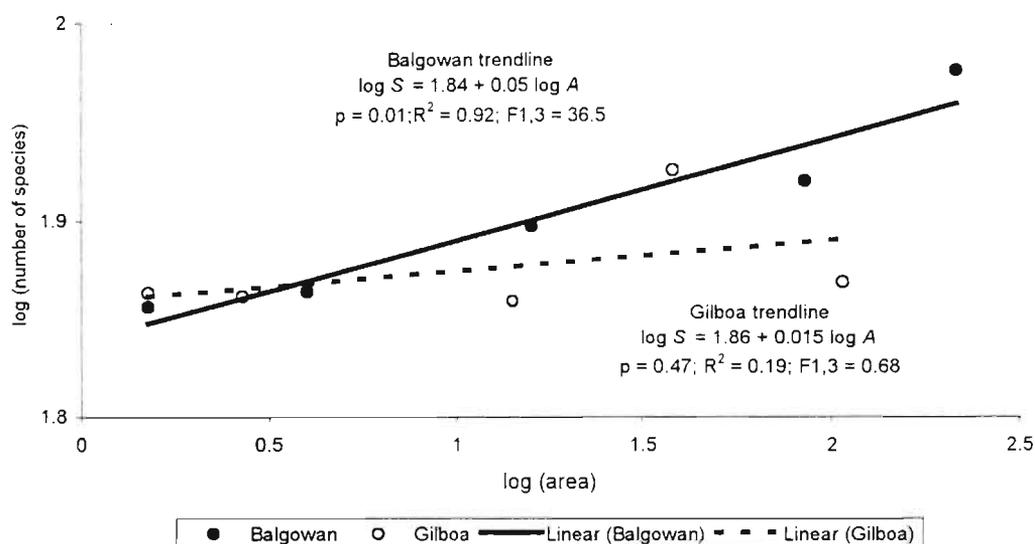
Fig. 3. Log - log species richness (rarefaction estimates, each forest standardised to 2311 individuals) regressed against forest area (logged value).

Smaller forests in both complexes have similar point diversity and rarefacted species richness at the quadrat level seems to be unaffected by the surrounding matrix type. There was considerable residual variance in species richness in the Gilboa complex, and only 18% of this variation was accounted for by change in area, whereas 90% of the variation in species richness was accounted for by the variation in area of patches in the Balgowan complex. It is therefore a possiblity that area was not affecting rarefacted epigaeic invertebrate species richness in the Gilboa forests while it was in the Balgowan forests.

3.2. Epigaeic invertebrate diversity

3.2.1. Species richness and abundance

There was no difference among forests from both complexes in species richness at a point i.e. local quadrat species richness, including Leopards Bush (Table 2).

Table 2. Diversity indices (per quadrat) and probability values for Balgowan and Gilboa forest complexes, and Karkloof. Comparisons were made using one-way anovas in MINITAB release 13.1.

	Probability value (P)	Karkloof (n = 18 quadrats) Mean ± StDev	Gilboa (n = 21 quadrats) Mean ± StDev	Balgowan (n = 21 quadrats) Mean ± StDev
Species richness / quadrat / week.	0.1	59.8 ± 6.6	55.5 ± 7.2	58.7 ± 5.4
Number of individuals / quadrat / week	0.007	329.4 ± 61.3	349.7 ± 118.9	256.8 ± 93.1
Shannon-Wiener diversity index (H')	< 0.001	3.0 ± 0.2	2.6 ± 0.2	3.0 ± 0.35
Pielou's evenness index (E1)	< 0.001	0.73 ± 0.05	0.65 ± 0.06	0.73 ± 0.08
Hill's number (N1)	< 0.001	20.5 ± 4	14.1 ± 3	21 ± 6
Hill's number (N2)	< 0.001	11.7 ± 3.4	6.6 ± 2.4	10.7 ± 4.2
Alpha index (α)	< 0.001	21.7 ± 3.9	19.3 ± 3.5	25.5 ± 5.7

In the Karkloof and Balgowan forests individuals were more evenly distributed among species than in the Gilboa complex (Pielou's evenness index - E1; Table 2). Balgowan had significantly greater species diversity than both Karkloof (p = 0.03) and Gilboa (p = 0), although this is probably a consequence of low point species abundance in the Balgowan. Gilboa and Karkloof species diversity did not differ statistically (Table 2, α-index).

3.2.2. Species turnover

The average species richness per quadrat as a percentage of the total species richness obtained from a forest was 40% for Gilboa and 41% for Balgowan. This suggests a fairly patchy distribution of species throughout the fragments in each complex and a fairly high turnover rate between quadrats within each forest and complex (see eg. Kruger and Lawes, 1997). Karkloof shows a more even distribution of species (47%) than both complexes. Whittaker's (1960) measure of species turnover (βw or β-diversity) was 1.1 for the Karkloof forests, 1.5 for the Gilboa forests, and 1.4 for the Balgowan forests, thus confirming a higher species turnover rate in the Gilboa forests.

3.3. Species-area trends of epigaeic invertebrate communities

The total number of epigaeic invertebrate species (collectively) in a forest was dependent on area in the Balgowan complex (Slope = 0.067; $F_{1,3} = 19.37$; P=0.02) (Fig. 4), and independent of area in the Gilboa complex (Slope = 0.089; $F_{1,3} = 6.77$; P=0.08). The slopes of the two regressions were significantly different ($t = 0.028$; $df = 6$; P < 0.05). These findings suggest that the pine matrix was influencing epigaeic invertebrate species richness in mistbelt mixed *Podocarpus* forest fragments. Those forests surrounded by the natural grassland matrix (Balgowan fragments) had much lower residual values than those surrounded by the unnatural pine matrix (Gilboa forests), implying that the pine matrix was overriding the influence of area, all other things being equal. In addition, all fragments save the second largest fragment that were surrounded by pine supported fewer species than those surrounded by grassland (Fig. 4).

The fly and ant communities in the Gilboa complex, and the beetles in the Balgowan complex yielded a significant positive species-area regression (Table 3), while the epigaeic invertebrate predators as a group showed no response to increasing area in either complex (Fig. 5).

Table 3. Species-area regression results for selected epigaeic invertebrate taxa, illustrating the lack of an area effect on the species richness for the majority of taxa.

Complex	Taxon	Slope	Probability value (p)	Df	$F_{1,3} =$	R^2
Balgowan	All	0.07	0.02	4	19.4	87
	Predators	0.05	0.1	4	4.25	59
	Beetles	0.1	0	4	98.9	97
	Flies	0.02	0.17	4	3.1	51
	Bugs	0.03	0.6	4	0.3	8
	Spiders	0.05	0.46	4	0.7	19
	Ants	0.04	0.21	4	2.5	46
Gilboa	All	0.09	0.08	4	6.77	69
	Predators	0.1	0.1	4	4.92	62
	Beetles	0.03	0.27	4	1.83	37
	Flies	0.09	0.05	4	10.8	78
	Bugs	0.1	0.4	4	1	25
	Spiders	0.12	0.2	4	2.6	47
	Ants	0.13	0.05	4	9.8	77
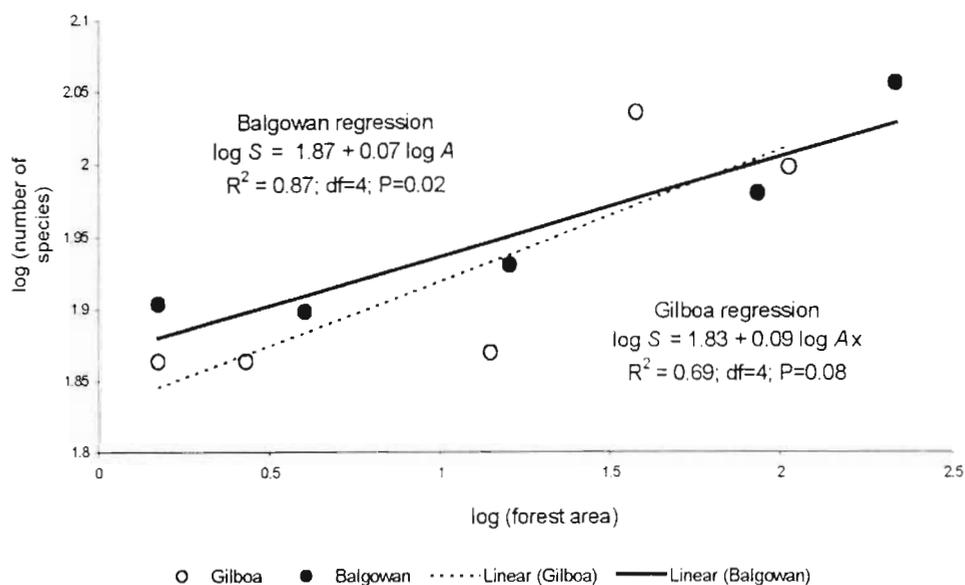
Fig. 4. Log-log species-area regression for the epigaeic invertebrate communities of Balgowan and Gilboa complexes.
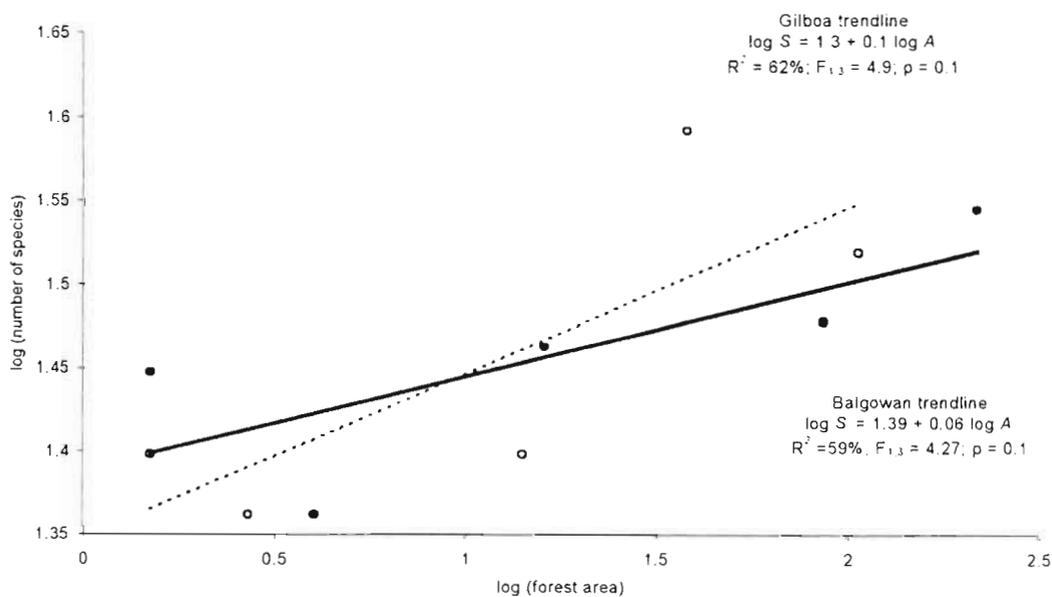
Figure 5. Log-log species-area regression for predaceous species illustrating lack of area effect on species richness.

3.4. Is there density compensation in the forest fragments?

Since density compensation should only occur when communities are saturated with species, and their respective densities are relatively high to account for the adjustments necessary for co-existance (Lawes and Eeley, 2000), an analysis using only those species common to all forests was deemed appropriate for assessing density compensation. The presence of rare species i.e. those that live naturally at low density and have life histories adapted to this lifestyle, may underestimate the level of density compensation occurring across the community (Lawes and Eeley, 2000). A least-squares untransformed regression revealed a significant negative relationship between the total density of invertebrates common to all forests and species richness for the Balgowan epigaeic invertebrates (Fig. 6). The Gilboa epigaeic invertebrate densities, on the other hand, exhibited a non-significant, positive relationship with species richness. These data suggest that density compensation in the Balgowan, and the lack thereof in the Gilboa, is generally an area dependant phenomenon operating at the landscape-level, and controlled by differences in species richness between forest fragments.
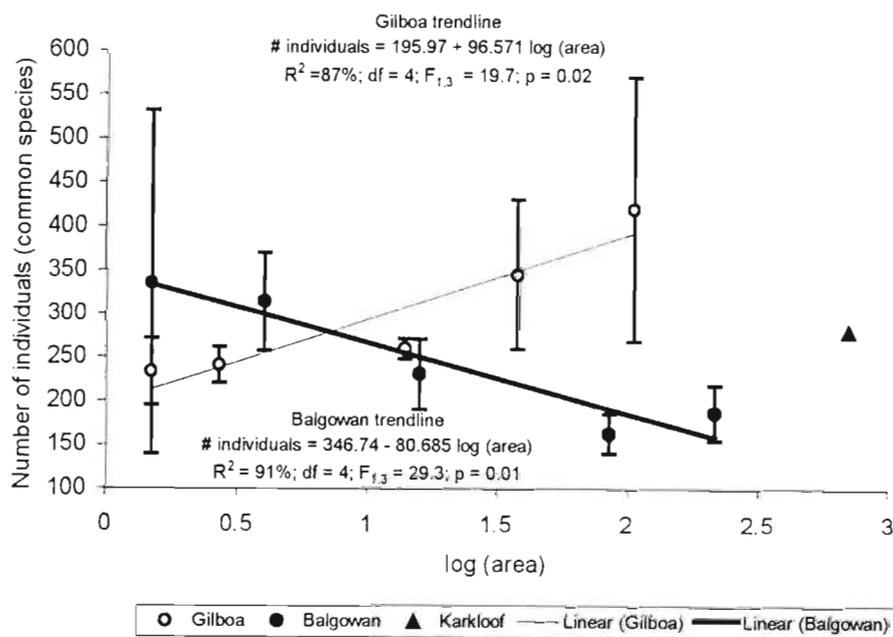
Fig. 6. Total density (individuals per $9m^2$) of epigaeic invertebrate species common to all forest fragments (including the control) versus log (area). Standard deviation is denoted by .

3.5. Habitat heterogeneity

The principal components analysis ordination plot of the standard deviations of the habitat variables revealed that the forests (Karkloof, Balgowan "A", Balgowan "B", Gilboa "B") were not significantly more heterogenous than smaller forests, as would be expected, although the Gilboa complex had a wider range of habitat heterogeneity scores than Balgowan forests (Fig. 7). The Karkloof gradsects were tightly clustered indicating a relatively homogenous habitat as would be expected in a single large forest. Regressing species richness and the α diversity index against habitat heterogeneity (PCA axis 1 scores) also did not yield significant results at the 0.05 probability level (i.e. 5%) for either complex. Habitat heterogeneity does not explain the variation in species richness among forests observed in this study. However, forest fragment Gilboa "C", had a patchy leaf-litter cover, and this may be responsible for it's low species richness.
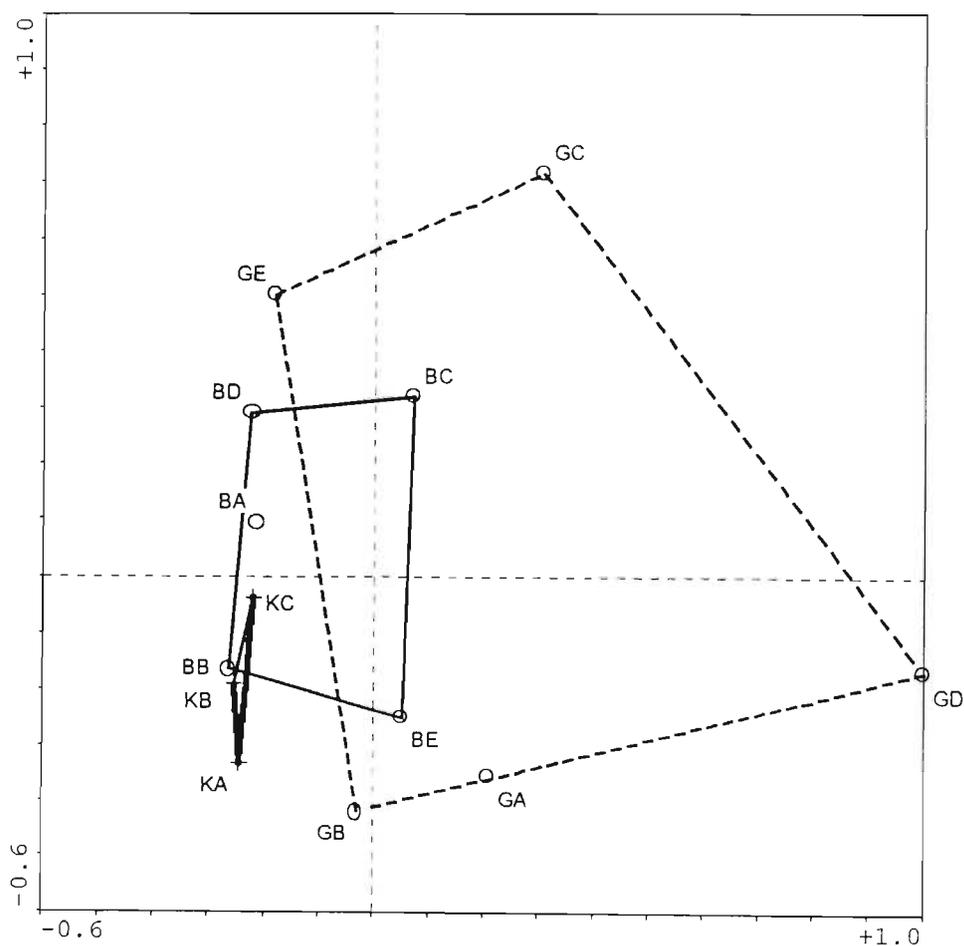
Fig. 7. PCA ordination diagram showing positions of forests by habitat heterogeneity.

4. Discussion

4.1. Species richness and diversity

Overall, Leopards Bush, the Balgowan and Gilboa forests had similar species richness per quadrat. The Balgowan complex, however, had significantly lower overall abundance (per quadrat) than both Leopards Bush and the Gilboa complex. However the Gilboa complex was significantly less diverse in epigaeic invertebrates, and contained fewer common species than Leopards Bush and Balgowan. This was a result of the small (< 30ha) Gilboa forests containing significantly less species than any of the other forests (grouped by area), and may have resulted from the patchy distribution of leaf litter on the forest floor. Smaller forests in both the Gilboa and Balgowan complexes exhibited significantly lower turnover rates than the larger forests, and this may have been a symptom of converging species assemblages through deterministic extinctions.

4.2. Species-area relationships

In a study assessing the impacts of fragmentation of *Eucalyptus* forests in Australia on beetles, Davies *et al.* (2001) showed that fragments surrounded by a pine matrix did not reveal a significant species-area relationship. This could have been the result of reduced dispersal between fragments eventually leading to extinctions and decreased abundance (e.g. Hanski and Thomas, 1994), although these extinctions had not yet taken place. Alternatively, dispersal between habitat fragments was not reduced because the matrix was not inhospitable to fragment-inhabiting species. In the current study, epigaeic invertebrate species richness increased with area in both Balgowan and Gilboa, but the effect of area was only significant in the case of the Balgowan complex, both for absolute and standardised (by rarefaction) species richness. Balgowan epigaeic invertebrates exhibited low residual values, while the species-area regression for Gilboa epigaeic invertebrate communities had large species residual values and so were not significant. Thus while traditional theories of island biogeography and species-area relationships may hold true for Balgowan, different processes are acting on the Gilboa epigaeic invertebrate communities, causing species richness to vary considerably around expected levels. Species richness is a highly area-dependent phenomenon in forests surrounded by grassland. In addition, area appeared to have little or no influence over species richness in forests surrounded by plantation and by implication, another more dominant effect is responsible for determining species richness. This is most probably a consequence of plantation forestry related disturbance, since all other factors are controlled for e.g. area, habitat heterogeneity.

4.3. Response of the predator guild to fragmentation

In this study, invertebrate predators were not significantly affected by area. Predators were selected as the top end of the food chain are usually more prone to extinction than species at lower levels because the former tend to have more unstable population dynamics and are less likely to persist in a fluctuating environment (Pimm and Lawton, 1977; Lawton, 1995; Holt, 1996). However, many predators are dietary generalists, including all of the spiders (Marc et al., 1999; Webb, 1989), centipedes (Lawrence, 1987), and many of the beetles (eg. Many staphylinid species – Bohac, 1999, Carabidae – Scholtz and Holm, 1985) and thus tolerate fragmentation effects better than dietary specialists. This functional group was therefore not the ideal choice for the aims of this study, although invertebrate predators in the Wog-Wog fragmentation experiment in Australia occurred at fewer sites after fragmentation (Davies et al., 2001). More specialized groups such as detritivores and fungivores may have been the better choice of functional group (Davies et al., 2001).

4.4. Density compensation in the forest fragments?

The epigaeic invertebrates of the Balgowan complex exhibit patch area-dependant density compensation (sensu MacArthur et al., 1972). MacArthur et al. (1972) found that island species generally had higher population densities than mainland species in the Pearl Archipelago off Panama. They suggested that species on small islands were subjected to lower levels of interspecific competition and predation, which allowed their populations to increase. However Schoener (1986) and Connor et al. (2000) argue that if total species density is independent of area, and if a species-area relationship exists, one need not infer competitive release to account for density compensation. However, species richness of epigaeic invertebrates of the Balgowan complex may have been dependent on area, and the species richness-dependent density compensation in the Balgowan complex would then suggest that the epigaeic invertebrate assemblages were approaching saturation if not already saturated with species. The epigaeic invertebrates of the Gilboa complex exhibited increasing population density with species richness. This is in agreement with a review by Connor et al. (2000) who found the same trend, albeit with a number of taxa (including invertebrates). This trend is inconsistent with the assumption of the equilibrium of island biogeography that population density is independent of area (MacArthur and Wilson, 1967). Furthermore, the tendency for population densities of individual species to be higher in larger rather than smaller areas suggests that density compensation is not a widespread phenomenon (Connor et al. 2000), and is consistent with the resource concentration hypothesis. This hypothesis attempts to explain the often-observed phenomenon that habitat patches with large amounts of resources, such as monocultures or large patches, have higher densities of insects (Root, 1973; Kareiva, 1983).

The overall positive correlation between population density and species richness in the Gilboa could arise from a number of mechanistic processes acting individually or in concert, and the mechanisms may differ among species (Connor *et al.* 2000). The enemies hypothesis and movement hypothesis (Root, 1973; Risch, 1981; Kareiva, 1983) could also explain this trend. Predation risk may be higher in small fragments, keeping the densities of prey populations low (Smith, 1974; Moller, 1991; 1995; Paton, 1994), or animals may be less likely to disperse from large fragments, keeping densities high (Raupp and Denno, 1979; Foster and Gains, 1991). As predators seem unaffected by area in this study, and knowing that the pine matrix is an inhospitable one, either scenario seems likely. Andren (1994) found that positive correlations between density and fragment area were more likely to occur in fragments embedded in highly fragmented landscapes. Evidence is mounting that the movement hypothesis may explain the positive correlation between population density and area (Raupp and Denno, 1979; Risch, 1981; Kareiva, 1983; Foster and Gaines, 1991). If this is the causal mechanism for the trend shown by the Gilboa epigaeic invertebrates, then it points directly to the pine matrix further isolating indigenous forest fragments, thus limiting dispersal between mistbelt mixed *Podocarpus* forest fragments. Furthermore, a few large patches within a pine matrix may account for the regional abundance of a species, with small fragments contributing little to regional abundance and persistence (Conner *et al.* 2000). If this is true, then recolonisation dynamics may play a small role in the regional persistence of a species within a pine matrix, and persistence would be insured by the preservation of a small number of large habitat fragments containing large, extinction-resistant populations (Harrison, 1991).

4.5. Local dominance of species.

Disturbance of habitats alters species composition and community structure by altering the physical environment and altering the resource base. Thus, stenotopic species are expected to give way to more resilient or generalist species leading to dominance in one or a couple of the most successful competitors. Empirical evidence suggests that often a change that negatively affects one species benefits another (e.g. Didham *et al.*, 1998; Davies *et al.* 2001). This has been shown to be the case in numerous studies, over a wide range of faunas (e.g. birds, Johns, 1991; aquatic invertebrates, Fowler and Death, 2000; Miller and Golladay, 1996; epigaeic invertebrates, Halme and Niemelae, 1993; Lenski, 1982; Samways, 1984; 1997)

Talistroides africana and *Tetramorium avium* dominated epigaeic invertebrate abundance in both Gilboa and Balgowan, although to a lesser degree in the Balgowan complex. In the Karkloof, a less disturbed mistbelt mixed *Podocarpus* forest habitat, dominance was shared with two other species. Thus there appears to be a trend toward the coexistence of more species with fewer species dominating in forests that are less disturbed. An example of this dominance (albeit over a short term) was observed by Neumann (1991) in

Australian *Eucalyptus* forest. Within four weeks after a wildfire there was a marked increase in the abundance and dominance of the seed-feeding ant *Prolasius pallidus*. This dominance was temporary, and this species was replaced by *Iridomyrmex foetans*, another foraging ant. Recolonisation of certain groups, such as the beetles, bugs and ants showed a predictable sequence with forest succession due to competitive exclusion (ants) or increases in resources (e.g. green foliage – bugs) (Neumann, 1991). After 12 months, many non-insect taxa that were in the forests prior to the fire had still not reestablished themselves, while the insect taxon richness had recovered to pre-fire levels, with only the Thysanoptera not recolonising the burnt areas.

The dominant ant species in all the forests in this study and second most abundant epigaeic invertebrate was *Tetramorium avium*. *T. avium* is generally a highly dominant species (Kempton, 1979; May, 1981), and made up 72.5% of ant abundance in the Blinkwater forest (surrounded by plantation) during a study by Kotze and Samways (1999), appearing to exclude other ant species since ant diversity was comparatively low in this forest (see also Belshaw and Bolton, 1993 for ecological dominance due to social structure; Hahn and Tschinkel, 1997 for competitive exclusion; Simberloff, 1976).

4.6. Habitat heterogeneity

The habitat diversity hypothesis proposes that as the area sampled increases, so new habitats are encountered (Giller, 1984), and more complex habitats have lower extinction curves (MacArthur *et al.*, 1972). Thus increased habitat diversity or heterogeneity will lead to increased species richness on habitat islands (Connor and McCoy, 1979; Schoener and Schoener, 1983). In this study levels of habitat heterogeneity were independent of forest area in both the Balgowan and Gilboa complexesand did not significantly affect the α diversity index or species richness of epigaeic invertebrates in either complex. These results agree with those obtained in the Knysna forest by Koen and Crowe (1987) who concluded in their study that vegetation structure and composition variation did not appear to influence forest invertebrate (or bird) communities. This may mean that (i) the major habitat variables responsible for shaping these epigaeic invertebrate communities were not included in the analyses, or (ii) that the epigaeic invertebrates as a whole do not need a complex habitat to survive, or (iii) that patterns are confounded by the use of whole communities and where a number of guilds are combined (Nummelin, 1996; Kotze *et al.*, 2000). This last point is emphasized by Ghazoul and Hellier (2000) in their review of invertebrate responses to logging.

4.7. The matrix effect.

The matrix has three potential roles in the formation of communities in fragments (Davies *et al.*, 2001). The first is altering dispersal and colonisation rates, which may be

reduced or enhanced depending on the dispersal characteristics of each species. Second, the matrix may provide an alternative habitat to existing species; for some species the matrix may be of lower quality than the original habitat, while others it may be of higher quality, and third, it may provide a source of invading species (Didham, 1997; Fahrig and Merriam, 1994; Shmida and Wilson, 1985). Timber plantations affect biodiversity structure by changing vegetation structure in the planted areas from an open graminaceous form to a woodland form, by altering the distribution, biomass and abundance of grassland plants, animals and micro-organisms, and thereby affecting demographic and ecological processes (Armstrong et al., 1998). It is clear that a pine matrix affects the expected species richness patterns of invertebrates. In a study that is currently underway, both *Talistroides africana* and *Tetramorium avium* showed clear preference for mistbelt-mixed *Podocarpus* forest over pine plantation and grassland (Wildy unpublished data). The surrounding pine may prevent these species from dispersing away from the larger indigenous forest fragments, thus concentrating species abundance and accentuating the dominance of these species.

Large, mature plantations have been called "biological deserts" and patches of indigenous vegetation within a pine matrix have been likened to "habitat islands" in an "inhospitable sea" (Armstrong et al., 1996a). While areas planted to pine undergo a drastic reduction in plants, birds and small mammals (Armstrong et al., 1996a) adjacent habitats are also affected. In Jonkershoek state forest, in the Western Cape, 35 years of pine afforestation reduced the number of indigenous plant species in an isolated area of mesic mountain fynbos by 58% (Richardson and van Wilgen, 1986). The mean cover of the native vegetation was reduced from 75% to 20%, and the mean native plant density was reduced by 66%. In a study done by Armstrong et al. (1996b), the number of plant species pollinated by insects dropped from 212 in natural fynbos to 82 species in the pine plantations themselves. Although these reductions may not be as high in the Afromontane region of KwaZulu-Natal province, the latter example nevertheless emphasizes the inhospitable nature of pine plantations, even for mobile species such as birds (Wethered, 2001), and therefore the importance of those remaining indigenous habitat patches.

To conclude, the pine matrix is affecting epigaeic invertebrate communities, generally increasing species abundance in larger mistbelt fragments. Area effects have been masked by the overriding effect of the pine matrix. Epigaeic invertebrate communities in mistbelt mixed *Podocarpus* forests surrounded by the natural, historic grassland matrix tended to conform to traditional species-area processes. Mistbelt forests surrounded by pine less than 30 ha supported fewer species than forests of similar size in the grassland matrix. Forests within the grassland matrix displayed a significant species-area relationship, while no such relationship was detected for forests in the pine matrix.

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CHAPTER 5

Epigaeic invertebrate taxa as ecological indicators in mistbelt mixed Podocarpus forests, KwaZulu-Natal, South Africa: selecting a "shopping-basket" of ecological indicators

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Abstract

Over the last 100 years in KwaZulu-Natal, large areas of the historical grassland matrix within which indigenous mistbelt mixed *Podocarpus* forests are located, have been replaced by commercial forestry. While the grassland matrix is not without disturbance (fires, livestock), complete replacement by pine trees (*Pinus* patula) considerably alters the ecology of the landscape and its component habitats. The effect of the matrix type on epigaeic invertebrate fauna in indigenous forest is the focus of this study. Epigaeic invertebrate communities were sampled using pitfall trapping methods in 11 mistbelt mixed *Podocarpus* forests, half of which were surrounded by pine plantation. In addition a number of structural and physiognomic habitat variables in each forest were measured and these were incorporated in a multivariate analysis (canonical correspondence analysis) to calculate a disturbance index for each pitfall quadrat. The change in abundance of the epigaeic invertebrates to this disturbance was used to identify a suite of putative ecological indicator species. A "shopping basket" of eight selected ecological indicators were mostly unrelated species, including one ant species, one amphipod species, two fly species and four beetle species. All but two species (*Talistroides africana* - Amphipoda and Tipulidae sp. 1 - Diptera) showed decreasing abundance with increasing disturbance. This study lends support to the notion that single-species are not representative or reliable enough to be used as indicators of whole habitats. In addition, the importance of selecting and measuring the correct environmental variables as surrogates for disturbance measures is emphasised.

Keywords: Afromontane forest; disturbance; canonical correspondence analysis; epigaeic invertebrates; community similarity; indicator species.

1. Introduction

Whether or not invertebrates can be used as indicators or more specifically, ecological indicators (McGeoch, 1998), of environmental change and habitat quality, depends on the temporal and spatial scale of their deterministic response to change, and their relationship to the scale of the processes one wishes to assess (Weaver, 1995; McGeoch, 1998). Invertebrates are commonly extreme *r*-strategists and their communities are therefore strongly influenced by stochastic processes (Putman, 1994; Pyle *et al.,* 1981; Samways, 1990). Invertebrates have little or no density-dependent feedback on population numbers and consequently their populations often show little temporal or spatial stability in the long-term

(Huhta *et al.* 1967; Gibson *et al.,* 1992; Putman, 1994; Luff, 1996). Furthermore, generation times are short and many generations are completed within the period of any gross perturbation. Thus, invertebrate populations experience immediate selection pressure from instantaneous conditions and respond more rapidly to environmental changes than do vascular plants and vertebrates (Rosenberg *et al.,* 1986; Erhardt and Thomas, 1991; Kremen *et al.,* 1993; Oliver and Beattie, 1996a). Rapid response to environmental disturbance gives invertebrates the potential to act as early indicators of ecological or environmental change (Kremen, 1992; Kremen *et al.,* 1993; Basset *et al.,* 1998). However, because of the latter traits, invertebrates do not have the opportunity to respond, in any evolutionary (predictable) sense, to long-term disturbance effects (Putman, 1994). Consequently, invertebrates (at least at the species population abundance level) may not be ideal indicators of long-term environmental change.

In terrestrial habitats, invertebrates are easily sampled and thus have the potential to provide data more useful to short-term environmental monitoring, impact assessment, and conservation practice than inventories of vertebrates and flowering plants (Murphy and Wilcox, 1986; New, 1991; Brown, 1991; Kremen *et al.,* 1993). By definition an ecological indicator (*sensu* McGeoch, 1998) must respond predictably, in ways that are readily observed and quantified, to environmental disturbance or to a change in environmental state (e.g. Hellawell, 1986; Paoletti and Bressan, 1996). Ecological indicators are distinct from biodiversity indicators (McGeoch, 1998); while both are biological indicators, a biodiversity indicator is a group of taxa or functional group whose diversity reflects some measure of the diversity of other higher taxa in a habitat, or set of habitats (Gaston and Blackburn, 1995; Gaston, 1996).

Invertebrate taxa that have been used as ecological indicators include butterflies (see Bowman *et al.,* 1990; Kremen, 1992; Pinheiro and Ortiz, 1992; De Vries, 1987; Alonso-Mejia *et al.,* 1998), ants (Lobry de Bruyn, 1999), staphylinid beetles (Bohac, 1999), soil dwelling diptera (Frouz, 1999), isopods (Paoletti and Hassall, 1999) and earthworms (Stork and Eggleton, 1992; Paoletti, 1999; see also Duelli *et al.,* 1999; Kevan, 1999). However, because epigaeic invertebrates are such a diverse group, any single species may respond differently to disturbance than another (Ghazoul and Hellier, 2000). On the other hand, most leaf-litter invertebrates (i.e. epigaeic invertebrates) are unable to move away from and outdistance local disturbances (because many species rely entirely upon the resources provided by the organic leaf-litter layer) (Hammond, 1990; Holloway and Stork, 1991), and are thus limited in terms of their ability to track environmental change (cf. Thomas, 1994). Consequently, epigaeic invertebrates have to respond to pressure effects *in situ*, and a wider spectrum of species may show a common response to, and reflect current conditions within, the habitat. With this in mind, the nature and frequency of disturbance can determine community structure and composition.

In addition to the ease with which objective data are collected on epigaeic invertebrates using pitfall trapping techniques (Samways *et al.,* 1996; Duelli *et al,.* 1999), the following

reasons make them good ecological indicators: 1) they include some of the most studied terrestrial taxa e.g., carabid and staphylinid beetles, spiders, (Duelli *et al.*, 1999) and ants (Samways *et al.*, 1996); 2) they play an invaluable role in maintaining ecosystem processes, such as nutrient cycling and predation (Olsen, 1963; Giller, 1996; Bohac, 1999), and are sensitive to environmental changes (Greenslade, 1984; Anderson, 1990; Dangerfield, 1990; Majer, 1990); and 3) there are generally a greater number of individuals and a greater biomass of invertebrates in the top few centimeters of soil and leaf-litter than in the canopy (e.g., lowland rainforest of Indonesia, Holloway and Stork, 1991).

Given a range of environmental variables that result from disturbance and are used as surrogate measures of disturbance, a suite of ecological indicator species may give a more accurate indication of environmental stresses and change than a single indicator species or taxon. For example, Lenski (1982) recorded different responses to clear-cutting (harvesting) temperate forest in two predatory *Carabus* species (Coleoptera: Carabidae). One species showed little response while the other was less abundant in clearcut areas. Hammond (1994) called this the "shopping basket" approach, and advocated 'shopping baskets' of suitable taxa when there is difficulty in identifying a taxon that fulfils all the criteria necessary for the required bioindicator (ecological indicator cf. McGeoch, 1998).

In this chapter I examine the potential for a suite or "shopping basket" of epigaeic invertebrates from Afromontane mistbelt-mixed *Podocarpus* forest identified first to the morphospecies level and then as ecological indicators. Unrelated species were expected to form part of this suite, as taxonomically related species often respond in different ways and to differing degrees, to environmental disturbance. In addition, I examined the putative effect of the quality of the matrix surrounding indigenous forest patches on the diversity of these invertebrate communities. I expected those mistbelt mixed Podocarpus forest fragments in the pine plantation matrix (Gilboa fragments) to be more disturbed than those surrounded by grassland (Balgowan fragments), and the Karkloof forest to be the least disturbed in terms of the measured habitat variables. It was expected that the diversity of the invertebrates would fluctuate according to individual species-responses to the calculated disturbance, and hence that a suite of species would serve as environmental indicators of forest condition.

2. Method

2.1 Study area and sites

See Chapter 3, section 2.1

2.2. Invertebrate sampling

See Chapter 3, section 2.2

2.3. Measuring and estimating disturbance

With the lack of specialist knowledge on specific epigaeic invertebrate groups, and the lack of species-level taxonomy, many invertebrates cannot be identified to the species level. Even when species-level identification can be achieved, there is often very little information such as life-history traits, feeding guilds and functional roles, known about the species. This makes it impossible to use them as indicators unless it can be shown that they respond predictably to a given disturbance (McGeoch, 1988).

Disturbance in forest vegetation is difficult to measure because (i) the frequency of certain disturbances is low, (ii) the effect of disturbance on forest composition and structure can be long-lasting (Everard *et al.*, 1994), (iii) the dynamic nature of forest ecosystems makes it impossible to obtain a "pre-disturbance" condition for comparison and control purposes, (iv) forest systems are diverse, complex and long-lived, and their quantification is almost without limit (Attiwill, 1994), and lastly (v) natural disturbance is difficult to categorize because the causal factors of disturbance are both exogenous and endogenous and operate over a wide range of size, frequency, predictability, timing and magnitude (Attiwill, 1994). It is therefore important to select disturbance variables and measure them at the scale that is meaningful to the invertebrate taxa. Arthropod populations are very sensitive to changes in vegetation structure (Majer, 1985; Madden and Fox, 1997). Some disturbed areas have been shown to move through a predictable succession as they regenerate (Connell and Slayter, 1977; Twigg *et al.*, 1989). Plant height and cover increases with an increase in regeneration age, while the proportion of bare ground decreases, litter increases and the microclimate is more buffered (Majer, 1990). Organisms are thought to enter recovery succession when conditions become optimal for them (Fox, 1982, 1990; Majer, 1985). Increases in plant species diversity or structural diversity are often correlated with an increase of other organisms (Southwood *et al.*, 1979; Majer, 1990). Therefore, a suite of environmental variables important in the structuring of invertebrate communities was selected and measured in each forest fragment.

The floristics and the physiognomy of each forest patch were obtained by measuring selected environmental variables in 10 m x 10 m quadrats. These quadrats were coincident with the pitfall quadrats along each gradsect:

Woody species: All woody species (diameter at breast height (DBH) > 10 cm) and saplings (1 cm < DBH < 10 cm) within a quadrat were identified to the species level. The DBH was recorded using a 2 m diameter tape, and height was estimated visually. With the selective logging that took place in these forests (ca. 1860-1940), species composition and basal densities may have been altered, and mean canopy height may have been lowered due to the removal of the larger trees. In smaller forests, increased edge-induced disturbance may have emphasised this change. Young and Mitchell (1994) found an increased biomass of trees with a decreased mean size of individuals due to edge effects. Multi-stemmed trees were identified and counted, along with the number of stems and the estimated medial DBH for each multi-stemming tree. Multi-stemming of trees is commonly associated with forest

disturbance, and appears to be a survival strategy in response to disturbance (Holness, 1998).

Canopy cover: Canopy cover was measured at five random points in each quadrat using a moose-horn (Stromberg, 1995), and these data were used to calculate mean percentage canopy cover. Increasing densities of upper-story vegetation shades the understory vegetation and can influence the moisture content of the soil (Samways, 1996). For instance, soil under *Acacia mearnsii* (black wattle) becomes desiccated more quickly than when under grass (Versveld and van Wilgen, 1986). This has consequences for species less resistant to desiccation.

Each 10 × 10 m quadrat contained three randomly positioned 1 × 1 m sub-plots. Within each of these sub-plots, the following data were collected:

Herb and grass height and cover: Average herb and grass height and percent cover was estimated visually.

Leaf-litter depth: Many of the invertebrates collected using the pitfall method rely entirely upon the organic leaf-litter layer for the resources (Hammond, 1990; Holloway and Stork, 1991). Hammond (1990) found that 25% of the beetle fauna in the latter forest type were associated with the soil/leaf-litter for the major (feeding) part of their life cycle. The leaf-litter depth was measured using a steel rod, 4 mm in diameter, inserted into the leaf-litter until the harder soil layer was encountered. This depth was measured with a rule, and was repeated five times in each sub-quadrat, obtaining an average for each site. The percent leaf-litter cover was visually estimated in each 1 × 1 m quadrat.

2.4. Analysis

Complex attribute data, such as invertebrate or vegetation community data, are best summarised by ordination techniques (Ter Braak, 1987). Ordination aims to order samples and/or species along axes that represent the main compositional gradients in the data set, using abundance data for the *m* species in the *n* sample plots only (Økland, 1996). A PCA was used to identify those vegetation variables which had the most influence on the invertebrate data set, and those which exhibited colinearity with other variables, and reduce them to a manageable, yet still ecologically meaningful number (Ter Braak, 1995; Randerson, 1993). In correspondence analysis (CA), ordination axes are considered as latent variables, or hypothetical environmental variables, constructed in such a way as to optimise the fit of species abundance data to a unimodal (in this instance) model of how species abundance varies along gradients (Økland, 1996). Thus, the dispersion of the sites along the CA axes is at its maximum (Ter Braak, 1995). This ordination technique was used in conjunction with the constrained technique (Canonical Correspondence Analysis - CCA, Økland and Eilertsen, 1993; Økland, 1996) to assess the degree to which the environmental variables correlated to the theoretical values generated by the unconstrained ordination technique (CA). Low eigenvalues of unconstrained axes relative to constrained axes (see below) should indicate

that the most important explanatory environmental variables have been included (Økland, 1996)

A single (combined) measure of forest disturbance was estimated for each quadrat using multivariate canonical correspondence analysis (CCA) (CANOCO program, Ter Braak and Smilauer, 1999). Canonical correspondence analysis, a method of direct or constrained gradient analysis (Ter Braak, 1996; Økland, 1996), allows one to analyse and visualise the relationship between species presence or abundance and environmental data from the same set of sample plots (Gauch, 1982; Ter Braak, 1987; Pollet, 1992), and so allows invertebrate responses, in this case, to be related directly to the degree of disturbance (Basset *et al.*, 1998). Canonical correspondence analysis (CCA) is used effectively on species-environmental data because species tend to have a single-peaked (unimodal) response to environmental variables (Ter Braak, 1987). This multivariate technique selects the linear combination of environmental variables that maximize the dispersion of the species scores, along the first CCA axis (Jongman *et al.*, 1987; Ter Braak and Prentice, 1988; Palmer, 1992). Therefore by comparing the eigenvalues of the ordination axes under unconstrained circumstances (CA) to those constrained by measured environmental conditions (CCA), one can gauge whether the most important environmental variables have been included in the analysis as predictors of species abundance (Okland, 1996).

Using a Monte-Carlo procedure within the CANOCO program (Ter Braak, 1999), the significance of the CCA axis eigenvalues and thus the significance of the environmental factor in the ordering of samples or species along that axis could be tested (Ter Braak and Prentice, 1988).

In this study quadrats were used as the basic unit of analysis since invertebrate response to environmental disturbance was likely to be at the scale of the quadrat, rather than the forest. A CA and CCA were run, both at the order and morphospecies level. Rare species were not downweighted as these species may also show individual responses to disturbance. As there was a significant species-area effect (see Chapter 3) the CCA was run without the area variable to assess the other variables without its influence. The species which had 10 % or more of their variation accounted for by CCA axis 1 were selected as potential indicators of environmental change, and the CCA was then rerun omitting each of the selected species in turn to calculate a new independent disturbance axis. This independent disturbance axis was used in the species abundance/disturbance regressions. A best-fit line was then plotted of species abundance against increasing disturbance to describe each species response to disturbance.

3. Results

A total of 61 282 epigaeic invertebrates, representing 168 morphospecies (Appendix 1-3) were collected in 20 160 trapping nights (one trapping night is the equivalent of one trap set for a 24 hour period). The beetles had the most species (56 species; 17 153 individuals) followed by the flies (26 species; 11 103 individuals), the spiders (21 species; 1 733 individuals), the ants (12 species; 9 337 individuals), the bugs (12 species; 582 individuals) and the ticks and mites (10 species; 310 individuals). The landhoppers (Crustacea: amphipoda), consisted of one species, and was the most abundant invertebrate in the forests with 17 271 individuals (see Appendix 4 - identification of ants, beetles, flies, amphipods, hymenopterans, millipedes and snails).

3.1. Species dominance

Both the Gilboa and Balgowan complexes were dominated by two species. The amphipod, *Talistroides africana,* was the most abundant species (n = 8 378, Gilboa; n = 6 445, Balgowan), comprising over 30% of the total number of individuals in each complex (Chapter 3 - Figs. 2b-d), followed by *Tetramorium avium* (Hymenoptera: formicidae) comprising more than 10% (n = 3417, Gilboa; n = 1932, Balgowan) of the total number of individuals in each complex. In the Karkloof forest four species accounted for more than 10% of the total abundance. Amphipods made up 13.45% (n = 2448), followed by *Tetramorium avium* (12.5%; n = 2304), Sphaeroceridae sp. 2 (Diptera) (11.91%; n = 2167) and Staphylinidae sp. 4. (Coleoptera) (11.1%; n = 2020).

Although species accumulation curves did not asymptote (this is often the case with invertebrates, even with intensive sampling; Gotelli and Colwell, 2001), the first-order Jackknife procedure estimated that a large proportion (83 ± 2.72 %) of all epigaeic invertebrate species present were sampled during the study.

3.2. Multivariate analyses

The collinear or insignificant habitat variables identified by PCA were removed, leaving slope, grass cover and height, number of multi-stemmed trees, herb height and cover, leaf-litter depth and cover, number of sub-canopy trees, number of seedlings, number of canopy trees and canopy density (see Appendix 5). Balgowan, Gilboa and Karkloof were not separated by CCA ordination plots at the order level, and the ordinations were not significant (axis 1, p = 0.89; all axes, p = 0.78). This was probably due to the diverse nature of epigaeic invertebrate guilds within orders. This was again the case for most of the orders individually, with the exception of the ants and flies that were significant for CCA axis 1 and all axes together. The overall canonical correspondence analysis (CCA) for all the invertebrates was highly significant for both the first canonical axis (P = 0.015; F ratio = 4.192) and all canonical

axes (P = 0.015; F ratio = 1.184). The first canonical axis revealed a gradient from the relatively undisturbed Karkloof quadrats to the more disturbed Gilboa quadrats situated in the pine matrix, with intermediate disturbance values for the Balgowan fragments. This separation can be clearly seen in the ordination diagram (Fig. 1).
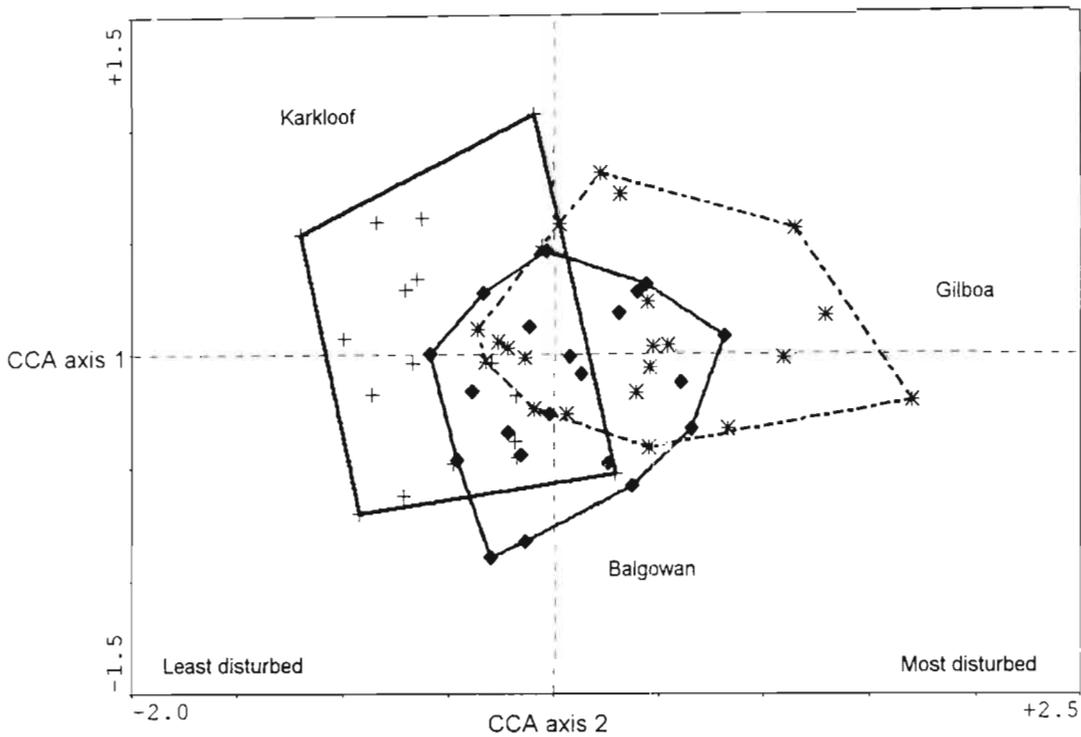
Figure 1. Canonical correspondence ordination illustrating a disturbance gradient from the least disturbed Karkloof (Leopards Bush) quadrats on the left to the most disturbed Gilboa quadrats on the right.

The sum of all canonical eigenvalues accounted for 27 % of the unconstrained eigenvalues. The first two eigenvalues of the CCA (λ_1 = 0.092 and λ_2 = 0.028) were considerably lower than those of the standard CA (λ_1 = 0.205 and λ_2 = 0.09), suggesting that one or more key environmental factors had been omitted from the analysis. The CCA ordination results did not improve with the inclusion of those environmental variables excluded after the PCA analysis. The "key" latent environmental variables may have environmental variables such as soil moisture or humidity that were not measured in this study. However, the selection of the variables considered in this study was based on current literature, and aimed at the level of epigaeic invertebrate communities, while the number of variables included was limited by the time and economic constraints of this study.

3.3. Disturbance characteristics

The more disturbed of the 60 quadrats were predominantly located in those forests surrounded by pine plantations in the Gilboa complex, and typically had more multi-stemmed

trees, and well developed grass and herb layers (Fig. 2). Undisturbed Karkloof quadrats were typically more dense (vegetation cover) characterized by a deep, abundant leaf-litter layer, dense sub-canopy and an abundance of seedlings indicating high rates of natural regeneration (Fig. 2). Leaf litter depth was the only variable that significantly explained the variation of species along the first axis. Invertebrate morphospecies that had more than 10 % of their variation accounted for by CCA axis 1 were selected as potential ecological indicators of disturbance.
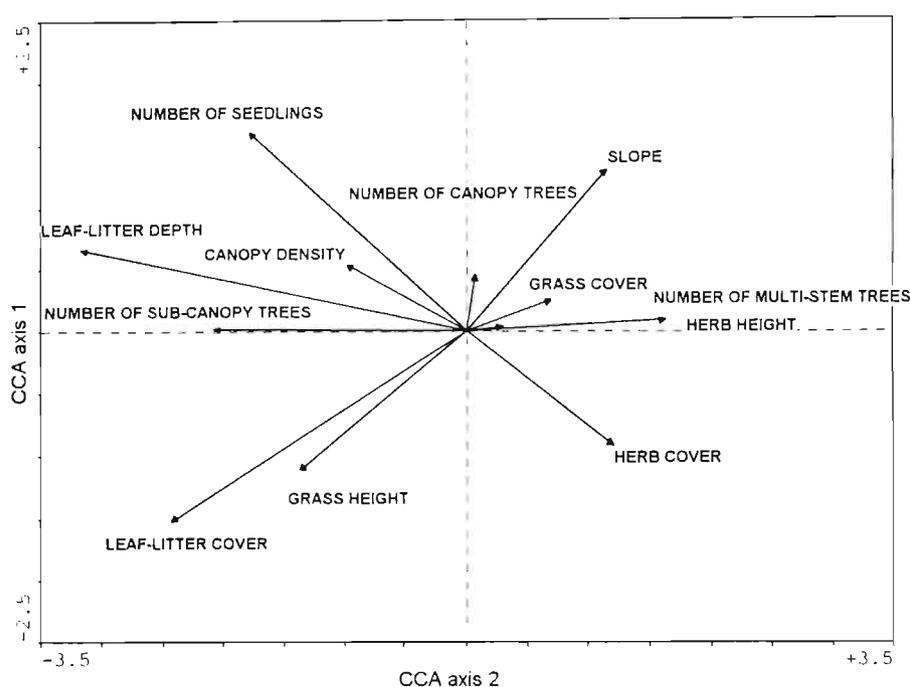
Figure 2. CCA ordination diagram indicating direction and strength of measured habitat and environmental variables.

3.4. Invertebrate response to disturbance

Invertebrate abundance typically decreased as disturbance increased (Table 2), with the exception of *Talistroides africana* (D1) and Tipulidae sp 1 (C7). All regressions were significant (Table 2), with Staphylinidae sp. 4 (B6) abundance most highly correlated to the disturbance axis (R^2 = 37%), followed by Staphylinidae sp. 12 (B38 - R^2 = 36%) and Carabidae sp 1 (B13 - R^2 = 35%) (Table 2). The regression plot for *Talistroides africana* was also significant ($P < 0.05$) and the abundance of this species was also highly correlated to disturbance relative to the other species (R^2 = 29 %) (Table 2). *Talistroides africana* occurred in much higher concentrations than any of the other potential indicators, and was therefore a more robust indicator, and would be the species used if a single organism were to be selected for indication of habitat quality (but see discussion).

Table 2. Indicator species selected for "shopping basket". "# Quadrats" refers to the number of quadrats (n = 60) that the species were present in. "Slope" refers to the slope of the linear regression line, followed by its significance, "P" (probability value) and "F" and correlation score "R²". "% variance" refers to the amount of variance accounted for by CCA axis 1 for that species.

SPECIES	# QUADRATS	SLOPE	P	$F_{1,58}$	R^2	% VARIANCE
Tetramorium avium (A4)	48	-2.5	0.004	9.26	14	18
Talistroides africana (D1)	60	50.8	0	24.03	29	33.8
Tipulidae Sp. 1 (C7)	58	2	0.005	8.7	13	27
Sphaeroceridae Sp. 2 (C27)	60	-15.6	0.001	13.02	18	19
Staphylinidae Sp. 4 (B6)	60	-11.8	0	33.56	37	35.8
Staphylinidae sp. 12 (B38)	37	-2.3	0	32.37	36	12
Carabidae sp. 1 (B13)	46	-3.5	0	31.63	35	10
Staphylinidae sp. 5 (B11)	51	-2.8	0	21.86	27	17

Furthermore, Staphylinidae sp. 4 (B6), Talistroides africana (Amphipoda: D1) and Sphaeroceridae sp. 2 (Diptera: C27) were present in all quadrats with fairly high maximal abundances. Opilionidae sp. 1 (Opiliones: L13) had a maximum medial abundance (hereafter: abundance) of two individuals in all the quadrats, and so were discarded as they were not useful indicators of habitat quality in this study. The same reasoning was applied to Gryllidae sp. 1 (Orthoptera: G1) and Melolonthinae sp. 2 (Scarabaeidae: B61) which had abundances of eight and four individuals respectively.

4. Discussion

4.1. The morphospecies concept

Morphospecies are taxa that are readily separable by morphological differences that are obvious to individuals without extensive taxonomic training (Oliver and Beattie, 1993). The use of morphospecies stems from taxonomic (see Lawton et al., 1998) and logistic constraints when processing vast quantities of data using conventional taxonomic methods (Pik et al., 1999). Even in temparate regions, producing complete invertebrate species inventories is not feasible without the allocation of many human and financial resources (Disney, 1986; Hammond, 1990; Di Castra et al., 1992; Lawton et al., 1998). In the absence of species level identification, morphospecies and genus-level identification give fairly accurate estimates of species richness (Pik et al., 1999), and morphospecies additionally give a good indication of species abundance. Pik et al. (1999) found the assessment of differences in an ant community identical regardless of whether species or morphospecies were used. These results support an earlier study by Oliver and Beattie (1996b) who showed identical characterization of communities with both species and morphospecies data in undisturbed Eucalyptus forests. The use of morphospecies is therefore taxonomically sufficient in these kinds of studies. There are, however, a number of criticisms of the use of morphospecies, including the fact that life histories of individual morphospecies and therefore their ecological importance is unknown (King et al., 1998; Hamer and Slotow, 2000). However, species level identification is often unhelpful due to the lack of knowledge of many species' habits and life

histories, and because differences between similar species are often ecologically insignificant. This limitation in species-level ecology negates the possibility of guild classification (an alternative to morphospecies classification) except by morphological characteristics such as mouthparts or other adaptations such as raptorial forelegs (predators).

At higher taxonomic levels (e.g. Order), intra-level variation (i.e guilds, functional roles) is so great as to be ecologically meaningless, with one group of organisms often spanning a large number of guilds, or undertaking a number of functional roles. Therefore in the absence of detailed invertebrate taxonomy, potential indicators in this case were effectively processed using the morphospecies approach (see Ellis, 1985; Pik *et al.,* 1999 on taxonomic sufficiency). Furthermore, this study illustrates how ecological indicators can be meaningfully selected using the morphospecies method and then, once selected, be further identified. The costs in terms of effort, time and money are hereby considerably reduced. Although morphospecies show a high correlation to species richness and diversity (Pik *et al.,* 1999), the classification of morphospecies will differ between scientists who have different classification criteria and levels of expertise. Therefore comparative studies will not be viable unless the same reference collection is used, or species-level identification is undertaken, at least in the final stages of assessment.

4.2. The ecologists' toolbox: indicator species

Monitoring and managing all aspects of biodiversity, including species richness and composition, physical structure and processes, is not viable. A number of methods have been proposed whereby attention is focussed on representative species (Simberloff, 1998). One such approach is the use of indicator species. As discussed by Landres *et al.* (1988), the idea of indicator species is a relatively well established (Hall and Grinnell, 1919) and is intuitively pleasing because management for many species may be simplified and made more cost-effective by considering only a single or small group of indicator species. However, Landres *et al.* (1988) question the validity of assuming that maintaining habitat quality for the indicator will be suitable for other species, an implicit assumption in the selection of ecological and biodiversity indicator species (see McGeoch, 1998).

Use of single species as bioindicators has thus been criticised by a number of authors (Kremen, 1992; Lawton *et al.,* 1998; Lombard, 1995; Prendergast and Eversham, 1997), and indeed, in the case of this study, a single-species ecological indicator would not be representative. Hammond (1994) suggested using a number of species (or "shopping basket") as indicators to represent a limited set of other taxa, and this approach is widely advocated (McGoegh, 1998; Hammond, 1994; Kotze and Samways, 1999; Chase *et al.,* 2000). In this study epigaeic invertebrates were identified to morphospecies due to reasons discussed above. There are a number of alternatives to species-level identification of invertebrates when looking for suitable indicators: identification to higher taxonomic level (family, genus), identification of feeding guilds (Verner, 1984, Block *et al,* 1986), functional

groups or morphospecies. However, there are considerable difficulties in extrapolating between guild members (Caro and O'Doherty, 1999) because (i) the factors that influence their respective populations may differ and are often unknown, (ii) they may show only partial overlap in niche or habitat, and (iii) there are practical difficulties in identifying the time course over which the changes in the population size of one species reflect those in another (Swanson, 1998; Temple and Wiens, 1989; Verner, 1984).

In the present study, if one were to choose a particular related group or family as an ecological indicator in this study, the rove beetles (Staphylinidae) would be the obvious choice. The family is represented in all of the forests and quadrats and makes up four of the seven morphospecies in the "shopping basket" of indicators listed above. They are the most abundant coleopteran family, are active on the soil surface, and so are readily captured using pitfall trapping methods (Buse and Good, 1993).

Another group that would be given careful consideration are the ground beetles (Carabidae). The carabids have been used extensively as indicators (Burel and Baudry, 1994; Butterfield et al., 1995; Butterfield, 1997; Eyre et al., 1996; Lenski, 1982; Luff, 1996; Ranta and As, 1982; Rykken et al., 1997), and are taxonomically and ecologically well known, especially in Europe. As a group they are sensitive indicators of temperature and moisture gradients, and different habitat types support distinct, identifiable communities (Thiele, 1977). Lovei and Sunderland (1996), however, argue 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. Interactions such as these may confound the effects of disturbance, making interpretations based on one or the other species temporally and spatially unstable.

Talistroides africana (Amphipoda) exhibit a significant, positive response to increasing disturbance, and the slope of the abundance/disturbance regression was very steep relative to the other species, indicating a high sensitivity and rate of increase in response to disturbance. This species would therefore have been the logical choice as a single-species indicator. However, Kotze and Samways (1999) found that the abundance of this species increased with increasing distance from the edge within Afromontane forest in one experiment (i.e. negatively correlated with edge-related disturbance), although in a later study (Kotze and Samways, 2001) found significantly more individuals at the ecotone than in the forest interior. This study showed a significant positive correlation with increasing disturbance (Table 2), and so these animals exhibit a wide, fairly unpredictable range of responses to fragmentation and disturbance of mistbelt mixed *Podocarpus* forest. It would therefore be unwise to use this species as a single indicator until more is known about factors affecting its abundance, and responses are more predictable.

4.3. Selecting the tools: the "shopping basket" of ecological indicators

Of the 16 morphospecies that were identified by the canonical correspondence analysis as potential ecological indicators, seven of them, G1 (Orthoptera), E4, E16, E11 (Hemiptera), C22 (Diptera), B61 (Coleoptera), A7 (Hymenoptera: Formicidae) were rejected as they were present in less than 50% of the quadrats. In addition, Opilionidae sp. 1 (Opiliones: L13) was removed due to it's low abundance. Tipulidae sp. 1 (Diptera:C7), Carabidae sp. 1 (Coleoptera: B13), Staphylinidae sp. 9 (Coleoptera: B38), Staphylinidae sp. 5 (Coleoptera: B11) also had low abundances (n < 20) in the quadrats, but were left in the "shopping basket" as they were still reliable indicators in this study, having high abundance-disturbance correlation scores. This study therefore demonstrates the importance of using abundance data rather than presence-absence data when assessing species responses to habitat disturbance (see also Kotze and Samways, 1999; Ghazoul and Hellier, 2000; Davies et al., 2001).

Spaeroceridae sp. 1 (Diptera: C27) and Staphylinidae sp. 4 (Coleoptera: B6) both had high abundances (n > 50), while *Talistroides africana* (Amphipoda: D1) had an abundance of nearly 350 individuals, and 29.3% of the variation in abundance was accounted for by disturbance. The response of *T. africana* to disturbance in this study was significant in terms of its abundance (Table 2), and this species was therefore included in the "shopping basket" of ecological indicators.

Kotze and Samways (1999, 2001) first discovered and then confirmed that *Tetramorium avium* is a forest edge species, most abundant between 8 m into the forest and 2 m into the grassland. As an edge species fragmentation effects should benefit these animals, especially in the smaller fragments which are essentially dominated by edge effects, or even the larger fragments if the edge effects reach further into the forests than the 32 m estimated by Kotze and Samways (1999). Davies et al. (2001) found edge effects influence epigaeic beetle abundance up to 100 m into Eucalyptus forests in Australia. Again, the results of this study suggest that the abundance of these ants decreased with increasing disturbance. This was not expected since these animals dominated the edges of the forest fragments studied by Kotze and Samways (1999).

Invertebrates and insects have been used in many studies as indicator species (Brown, 1997; Humphrey et al., 1999; Madden and Fox, 1997; Stork and Eggleton, 1992). In many instances groups of related species have been used as indicators, such as carabid beetles (Butterfield et al., 1995; Eyre et al., 1996; Luff, 1996; New et al., 1995; Pearson, 1994; Rykken et al., 1997) and butterflies and moths (Kitching et al., 2000; Erhardt, 1991). This study has shown that a group of essentially unrelated species are often more reliable than closely related species when assessing habitat disturbance.

In conclusion, the selected "shopping basket" of eight indicator taxa that showed response to disturbance were mostly unrelated species, including one ant species, one amphipod species, two fly species and four beetle species. This project lends support to the

idea that single-species are not representative or reliable enough to be used as indicators in studies such as these. In addition, the importance of selecting and measuring the correct environmental variables as surrogates for disturbance measures is emphasised.

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CHAPTER 6

Summary and conservation and management recommendations

The purpose of this study was to investigate the current status and diversity of epigaeic invertebrates in selected Afromontane mistbelt mixed *Podocarpus* forest patches. Specifically, I assessed the consequences of area reduction and matrix transformation, due to commercial forestry, on epigaeic invertebrate diversity, and the role of small forest fragments in their conservation. In the light of ongoing forest destruction and fragmentation, these data were used to provide guidelines for the management and conservation of Afromontane forest and for adjacent land-use planning.

Captured invertebrates were identified to morphospecies within their orders. Where possible, further identification was carried out. The reference collection is housed in the School of Botany and Zoology at the University of Natal, Pietermaritzburg.

A total of 61 282 epigaeic invertebrates, representing 168 morphospecies, were collected in 20 160 trapping nights (one trapping night is the equivalent of one trap set for a 24 hour period). The beetles were represented by the most species (56 species; 17 153 individuals) followed by the flies (26 species; 11 103 individuals), spiders (21 species; 1 733 individuals), ants (12 species; 9 337 individuals), bugs (12 species; 582 individuals) and ticks and mites (10 species; 310 individuals). The landhoppers (Crustacea: amphipoda), were represented by one species, and were the most abundant invertebrates in the forests with 17 271 individuals.

1. Species-area trends of epigaeic invertebrate communities within a fragmented forest landscape

In the Balgowan complex (grassland matrix), the overall number of epigaeic invertebrate species in a forest fragment was most probably area dependent, with smaller forest fragments supporting fewer species than larger fragments. In contrast, there was no significant effect of isolation on forest fragment species richness in the Gilboa complex (pine matrix), although these forests tended to support fewer species than their Balgowan counterparts.

The above illustrates the confounding influence of the pine matrix in the Gilboa complex over the "normal" species-area effects that are found in the Balgowan complex, since the matrix represents the single most important difference between the two forest complexes. It is therefore crucial to conserve the largest intact forest fragments in order to preserve overall epigaeic invertebrate species richness.

2. Density compensation in epigaeic invertebrate communities

Density compensation (decreasing species density with increasing species richness in a patch) in the Balgowan complex suggests that the epigaeic invertebrate assemblages are approaching saturation, if not already saturated with species. The epigaeic invertebrates of the Gilboa complex, on the other hand, exhibited increasing population density with increasing species richness. This lack of density compensation in the Gilboa could be explained by the "enemies hypothesis" or "movement hypothesis". Predation risk may be higher in small fragments, keeping the densities of prey populations lower in these fragments, or animals may be less likely to disperse from large fragments, keeping densities high. Under the "movement hypotheses", the pine matrix acts to further isolate indigenous forest fragments in the Gilboa. Recolonisation dynamics may therefore play a small role in the regional persistence of a species within a pine matrix, and persistence would be ensured by the preservation of a small number of large habitat fragments containing large, extinction-resistant populations. The establishment of ecologically functional grassland corridors (i.e. wide enough to maintain "natural" ecological processes) between mistbelt mixed *Podocarpus* forest fragments would facilitate dispersal of epigaeic invertebrates.

3. The impact of habitat heterogeneity on epigaeic invertebrates

Habitat heterogeneity was independent of forest area in both the Balgowan and Gilboa and did not significantly affect the α diversity index or species richness of epigaeic invertebrates in either complex.

4. Community similarity

Cluster analyses revealed that all forests were at least 60% similar in community diversity (Bray-Curtis cluster analysis), with only three pairs of forests having over 50% of species unique to one of the pairs (complementarity). Twenty-two percent (n = 37) of invertebrate species recorded were common to all forests and these shared species were generalist feeders: 14 predators (1 ant, 7 beetles, 5 spiders and 1 centipede), 13 decomposers (10 flies; larval phase, 1 amphipod, 1 millipede and 1 isopod); 3 phytophages (2 beetles and 1 cricket), 2 saprophages (bugs), 1 omnivore (cockroach) and 4 unidentified species. The large number of shared generalist species suggested that extinction-prone species had already become extinct in these fragments, giving way to more vagile, generalist or eurytopic species. As expected, the larger Balgowan forests situated within natural grassland were grouped with the Karkloof (control forest) while the two large Gilboa fragments, situated within pine plantation, were not. The effect of matrix type on diversity of epigaeic invertebrate communities was most notable for large forests (i.e. over 30 ha). Large

fragments with core areas unaffected by edge-induced disturbance would support more forest dependent species than small fragments due to a lower susceptibility to invasions.

5. The prevalence and implications of community nestedness

Although not significantly nested, epigaeic invertebrate communities in both forest complexes tended toward nestedness. Isolation of forest fragments appeared to play a lesser role than patch area in determining the invertebrate community composition. Assuming that communities are extinction-dominated, community convergence in small fragments has probably already occurred, with invasions from the matrix confounding patterns of deterministic extinction of forest-dependent epigaeic invertebrate species.

The question of how difficult it is for these animals to disperse through pine plantations compared to grassland remains unanswered. This study did not sample epigaeic invertebrates in the grassland and pine matrices to identify those species that have invaded the mistbelt forests, but this is a future research opportunity in this area.

6. Disturbance-induced dominance of epigaeic invertebrate species

Talistroides africana and *Tetramorium avium* dominated epigaeic invertebrate abundance in both Gilboa and Balgowan, although to a lesser degree in the Balgowan complex that was surrounded by grassland. In the Karkloof, in the least disturbed forest, dominance was shared with two other species. Hence, there appears to be a trend toward the coexistence of more species with fewer dominant species in forests that are less disturbed.

7. Disturbance and its impact on epigaeic invertebrate communities

A habitat disturbance gradient was evident from the relatively undisturbed Karkloof quadrats to the more disturbed Gilboa quadrats situated in the pine matrix, with intermediate disturbance values for the Balgowan fragments. Forest fragments within the disturbed Gilboa complex typically had more multi-stemmed trees and well-developed grass and herb layers. The undisturbed Karkloof forest was characterised by a deep, abundant leaf litter layer, dense sub-canopy, and an abundance of seedlings indicating high rates of natural regeneration. Leaf litter depth was the most important variable in explaining the variation of epigaeic invertebrate species. Epigaeic invertebrates proved to be a wise choice for ecological indicators at a general level, as the species-area relationships and density compensation trends mirrored those found in birds by Wethered (2001) in the same region.

A "shopping basket" of eight selected ecological indicators are mostly unrelated species, including one ant species, one amphipod species, two fly species and four beetle species. All but two species (*Talistroides africana* - Amphipoda and Tipulidae sp. 1 - Diptera) showed decreasing abundance with increasing disturbance.

This project lends support to the idea that single species are not representative or reliable enough to be used as indicators in similar studies.

8. Concluding Recommendations

i.   In both pine and grassland matrices, the conservation of large, intact forests, possibly at the expense of smaller fragments, is advised in order to conserve overall epigaeic invertebrate diversity.

ii. Where possible, natural corridors should connect Afromontane mistbelt mixed *Podocarpus* forests situated within a pine matrix in order to facilitate the movement of epigaeic invertebrates between them.

iii. Pristine grasslands are highly threatened in the Afromontane region. Kotze and Samways (2001) argue that these disturbances will continue to influence the character of the Afromontane/grassland interface, and ultimately the character of Afromontane forest. It is thus vital to conserve the grassland matrix as well as the forests themselves.

iv. Epigaeic invertebrates typical of undisturbed Afromontane forest require habitats with a fairly dense ground vegetation cover, with deep, abundant leaf-litter layer, dense sub-canopy and an abundance of seedlings indicating high rates of natural regeneration. Epigaeic invertebrates exhibit varied responses to disturbances. Hence, it is essential that decisions regarding the conservation of the Afromontane forest system be based on a suite of selected invertebrate ecological indicators rather than one species.

v.   In general, this study supports the wealth of evidence advocating the use of epigaeic invertebrates, especially Carabid and Staphylinid beetles, as ecological indicators. However, these groups should not be used in isolation where general management and conservation policies are concerned. The larger the "shopping basket" of indicator species is, the more applicable the resulting data will be regarding general conservation of forests and epigaeic invertebrate communities within them. In this study, eight species were identified by canonical correspondence analysis as ecological indicators that were sensitive to forest disturbance. This suite of species (abundance data) in the mistbelt mixed *Podocarpus* forests of the KwaZulu-Natal midlands will provide an accurate indication of forest condition in Summer.

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Appendix 1. Abundance (no. of individuals) of morphospecies identified in the Karkloof (control) forest.

Morphospecies		Karkloof (Control forest)																	
	Transect	A	A	A	A	A	A	B	B	B	B	B	B	C	C	C	C	C	C
	Quadrat	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6
Ants	A1	43	29	36	43	45	78	51	33	30	42	34	56	40	30	23	46	30	58
	A2	1	0	1	1	0	1	1	1	1	1	0	0	0	1	1	1	0	0
	A3	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
	A4	5	18	13	21	27	8	3	1	1	5	5	9	6	3	4	1	1	1
	A5	1	0	1	1	1	1	0	0	1	0	0	0	0	1	0	0	0	1
	A6	3	1	5	0	1	0	4	0	0	1	0	0	1	1	1	2	1	1
	A7	0	0	0	0	0	1	1	0	0	0	1	1	0	0	0	0	0	0
	A8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	A9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	A10	0	1	1	1	1	1	0	0	0	1	1	1	0	0	0	0	0	1
	A12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	A13	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Beetles	B1	20	67	29	32	13	37	29	8	24	12	8	11	16	14	25	9	13	10
	B2	3	6	1	1	1	1	2	2	0	6	2	3	2	1	2	1	2	1
	B3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	B4	1	0	0	1	0	0	0	0	0	1	0	0	1	0	0	1	0	0
	B5	5	16	18	11	8	9	14	8	9	16	13	12	15	9	12	12	14	5
	B6	51	20	52	42	42	27	38	20	34	50	46	57	29	26	20	29	31	26
	B7	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
	B8	19	17	18	18	8	5	0	2	2	1	2	1	1	1	0	2	2	1
	B9	6	9	8	11	8	6	1	1	2	1	1	1	2	1	3	1	1	1
	B10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	B11	2	7	6	15	15	6	0	1	3	8	6	13	4	1	1	13	14	6
	B12	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
	B13	19	2	6	2	9	1	18	10	15	5	4	3	7	4	10	6	9	4
	B15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	B16	2	1	1	1	1	3	0	2	3	2	1	9	2	1	1	1	3	2
	B17	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
	B18	0	1	1	0	2	1	0	1	1	1	1	1	1	1	1	0	1	1
	B19	0	0	1	1	0	1	1	0	1	1	1	1	1	0	1	0	0	0
	B21	4	4	2	4	2	2	8	3	10	3	6	3	14	4	3	6	14	2
	B22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	B23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	B24	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0
	B25	1	2	0	1	0	1	1	0	1	1	0	1	16	2	1	1	1	0
	B26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	B27	0	0	1	1	0	1	0	0	0	1	0	0	0	0	0	0	1	0
	B28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	B30	1	1	1	0	0	1	0	1	0	0	0	0	1	5	1	19	5	23
	B33	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
	B35	0	0	0	0	1	0	0	0	1	0	1	1	0	0	0	0	1	0
	B36	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	B37	8	4	1	11	3	1	2	2	1	1	1	1	2	3	1	1	2	1
	B38	1	2	4	1	3	1	3	10	3	1	2	3	2	7	19	4	3	6
	B39	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0
	B40	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	B41	0	1	0	0	0	1	0	1	1	1	1	0	0	1	1	1	1	1
	B42	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	B43	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
	B44	0	0	1	1	0	1	0	1	1	0	0	1	1	1	0	0	1	0
	B45	1	0	1	1	1	1	0	0	1	1	1	0	1	0	0	0	0	0
	B46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	B47	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
	B48	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
	B49	0	1	0	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0
	B50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	B52	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0
	B54	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1
	B55	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0
	B56	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	B57	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0
	B58	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	B59	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
	B60	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
	B61	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0
	B62	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0
	B63	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	B64	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 1 cont.

Morphospecies	Transect	A	A	A	A	A	A	B	B	B	B	B	B	C	C	C	C	C	C
	Quadrat	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6
									Karkloof (Control forest)										
Flies	C1	17	10	5	12	12	1	9	7	11	18	11	11	10	14	7	5	6	10
	C2	4	4	2	3	2	7	3	2	4	2	5	2	4	1	2	1	1	4
	C3	4	7	15	36	13	5	4	3	3	6	11	6	9	11	8	7	5	7
	C4	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0
	C6	3	1	1	1	1	1	2	1	1	2	3	1	2	3	1	2	1	1
	C7	1	1	1	2	1	1	1	1	2	1	1	1	1	3	1	1	1	1
	C8	6	1	3	1	3	2	1	2	3	3	4	3	1	5	1	1	1	3
	C9	2	3	1	3	1	1	1	1	3	3	2	2	1	2	2	2	4	2
	C10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	C11	1	1	1	1	2	1	1	1	0	0	1	1	1	0	1	1	0	1
	C12	1	1	1	1	1	1	0	1	0	0	1	1	0	0	1	1	1	1
	C15	4	6	5	3	1	1	1	1	1	3	1	0	3	0	0	1	1	0
	C18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	C19	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	C21	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
	C22	1	1	1	1	1	0	1	0	0	0	1	1	0	0	0	0	0	0
	C25	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
	C27	45	24	8	48	17	1	99	143	120	47	59	42	40	14	61	25	27	29
	C29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	C30	0	1	2	1	1	0	1	1	1	0	1	1	0	1	8	5	0	1
	C31	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
	C33	0	1	0	0	0	1	1	0	0	1	2	1	1	1	0	0	1	1
	C34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	C35	1	1	2	1	1	1	0	1	1	1	0	0	0	0	0	0	0	0
	C36	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	C37	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Land-hopper	D1	68	7	5	41	105	96	82	44	47	54	67	6	52	25	27	4	5	11
Bugs	E1	1	0	0	1	0	1	0	0	1	1	2	0	0	1	0	1	1	0
	E2	0	0	0	1	1	2	0	1	0	1	1	0	1	0	1	1	1	1
	E4	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0
	E5	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0
	E7	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
	E10	1	1	1	3	1	0	0	0	0	0	1	0	3	1	0	0	0	0
	E11	2	2	1	1	2	3	0	0	0	1	2	1	1	0	1	0	1	1
	E13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	E14	2	1	1	1	2	4	1	0	1	1	1	2	0	0	0	0	1	1
	E15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	E16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	E17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Earwigs	F1	1	0	1	1	1	0	1	1	0	1	1	1	1	2	0	1	1	1
	F2	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0
	F3	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0
Crickets and Grasshoppers	G1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	G2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	G4	3	2	2	2	1	1	1	2	1	2	1	1	0	1	1	1	2	2
	G5	1	1	1	0	1	1	0	0	0	1	0	0	1	0	1	1	0	0

Appendix 1 cont.

Morphospecies	Transect Quadrat	Karkloof (Control forest)																	
		A 1	A 2	A 3	A 4	A 5	A 6	B 1	B 2	B 3	B 4	B 5	B 6	C 1	C 2	C 3	C 4	C 5	C 6
Mites and Ticks	H1	1	0	1	0	0	1	1	1	0	1	1	0	0	0	0	0	1	0
	H2	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
	H3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	H4	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
	H5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	H6	1	1	0	0	0	0	3	1	1	1	0	0	0	0	0	0	0	0
	H7	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
	H9	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0
	H10	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
	H11	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1
Cockroaches	I1	2	1	1	3	1	2	1	1	3	2	2	1	1	3	1	1	1	1
	I2	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0
Wasps and Bees	K3	2	1	0	1	0	1	1	0	1	1	2	1	1	1	1	1	1	1
	K13	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
	K14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	K15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Spiders	L1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
	L2	0	0	1	0	0	0	0	0	1	0	1	0	1	0	0	0	1	0
	L3	2	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1
	L4	1	0	1	1	1	0	1	0	1	0	0	0	1	0	1	0	1	0
	L7	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0
	L8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	L9	3	1	1	5	4	2	4	1	2	5	8	6	3	1	2	1	5	6
	L10	0	0	1	0	1	1	1	1	1	1	1	1	0	1	0	1	1	0
	L11	2	1	1	2	0	1	1	1	1	1	0	1	1	1	2	2	1	1
	L13	1	0	2	1	0	1	1	1	1	1	1	0	2	1	1	1	0	1
	L14	1	0	1	1	0	2	1	0	1	0	0	0	0	0	0	0	0	0
	L15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	L16	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
	L17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	L18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	L19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	L20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	L21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	L22	1	0	1	0	1	1	0	1	1	0	0	1	0	1	1	0	1	0
	L23	0	0	0	0	0	0	0	1	1	1	0	1	0	1	0	0	0	1
	L24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Centipedes	M1	1	1	2	1	2	4	1	1	1	3	1	1	0	1	0	0	2	0
	M2	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	1	1
	M3	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0
	M4	0	0	0	0	0	0	1	0	0	0	1	1	1	0	0	0	0	0
	M5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	M6	1	1	1	0	1	0	2	0	1	0	0	0	1	1	0	0	1	1
Millipedes	N1	1	3	9	6	7	1	1	8	3	9	13	7	7	5	1	21	8	3
	N2	0	1	1	0	0	1	0	0	0	0	0	1	0	0	0	1	1	1
	N4	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0
	N5	0	0	0	0	0	1	1	0	1	2	1	0	2	1	1	1	1	1
	N6	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
	N7	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0
Woodlice	O1	2	1	3	2	1	4	7	1	5	4	4	3	3	2	3	2	1	2
	O2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	O3	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Pseudoscorpions	Q1	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0
Archaeognaths	T1	0	1	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0

Appendix 2. Abundance (no. of individuals) of morphospecies identified in forests of the Gilboa complex.

Morphospecies	Forest	A	A	A	A	A	A	B	B	B	B	B	B	C	C	C	D	D	D	E	E	E
	Quadrat	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	1	2	3	1	2	3
Ants	A1	94	19	34	157	150	43	39	72	92	101	60	37	27	28	21	22	31	28	32	36	30
	A2	0	1	1	1	4	0	1	1	1	1	0	1	0	0	1	0	1	0	0	0	0
	A3	0	0	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	A4	0	1	1	0	1	0	1	1	1	0	0	1	0	0	0	1	1	3	0	1	13
	A5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
	A6	0	0	0	0	0	0	1	1	0	1	1	1	1	1	1	3	0	0	0	1	0
	A7	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
	A8	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
	A9	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
	A10	0	0	2	1	1	0	1	0	1	1	1	1	0	0	0	1	1	0	1	0	0
	A12	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	A13	0	0	0	0	0	1	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0
Beetles	B1	22	5	28	39	37	41	40	25	21	25	33	39	27	15	13	12	19	29	28	14	32
	B2	0	0	3	1	0	1	3	1	7	5	2	2	2	0	1	2	0	1	2	4	4
	B3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	B4	1	1	1	1	0	0	1	1	1	1	0	0	0	1	0	1	0	1	0	1	1
	B5	15	4	11	14	13	10	17	8	14	15	7	5	19	4	6	8	7	7	6	6	6
	B6	10	6	30	48	22	7	12	3	18	12	11	2	12	7	8	4	3	11	6	2	2
	B7	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
	B8	5	2	13	9	12	1	5	2	18	10	3	1	5	4	2	4	2	6	21	8	16
	B9	25	3	19	4	9	12	45	15	43	39	12	6	3	14	10	7	5	5	34	24	1
	B10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	B11	1	1	0	10	7	1	0	0	9	3	1	1	1	1	1	0	1	1	1	0	1
	B12	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0
	B13	1	1	0	2	0	1	0	1	1	1	1	1	13	2	1	1	1	1	0	0	2
	B15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	B16	0	1	1	3	1	1	1	3	2	2	1	3	2	1	5	3	1	15	1	1	2
	B17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	B18	1	1	3	2	6	2	0	1	1	1	1	1	7	1	2	1	3	1	0	1	0
	B19	1	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	1	1	1	1	0
	B21	2	2	1	1	6	4	1	1	0	0	1	1	3	1	1	1	2	0	0	1	0
	B22	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
	B23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
	B24	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0
	B25	3	0	0	0	0	3	0	1	0	1	1	1	1	1	0	0	0	1	0	0	0
	B26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	B27	1	0	1	0	1	1	0	1	1	1	1	0	1	1	0	0	1	0	1	1	0
	B28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	B30	0	0	0	0	0	0	0	1	1	1	2	1	0	1	0	0	0	0	0	0	1
	B33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	B35	0	1	1	0	1	2	1	1	1	0	0	0	1	0	0	0	1	0	1	1	0
	B36	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	B37	0	1	1	1	2	1	1	0	0	0	1	0	0	0	0	1	1	1	0	0	1
	B38	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	B39	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	B40	0	1	0	0	0	1	0	0	0	0	0	0	1	0	1	1	1	0	1	1	1
	B41	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	1	1
	B42	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	B43	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	B44	0	1	1	0	1	0	0	0	1	0	0	1	1	1	0	0	1	0	0	0	1
	B45	1	1	1	1	1	1	1	1	1	1	0	1	0	0	0	0	1	0	1	0	0
	B46	0	0	0	0	1	0	0	0	1	0	1	1	0	0	0	1	0	0	0	0	0
	B47	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
	B48	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0
	B49	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0
	B50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
	B52	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	B54	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1
	B55	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	B56	0	1	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0
	B57	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
	B58	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	B59	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	B60	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	B61	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	B62	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	B63	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	B64	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 2 cont.

Morphospecies		Forest	A	A	A	A	A	A	B	B	B	B	B	B	C	C	C	D	D	D	E	E	E
		Quadrat	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	1	2	3	1	2	3
													Gilboa complex (commercial forestry matrix)										
Flies	C1		7	4	10	6	9	6	13	9	5	10	6	8	10	10	11	13	12	18	16	11	16
	C2		1	2	1	2	3	1	4	1	1	1	2	1	1	0	0	4	2	1	1	1	1
	C3		12	7	1	5	7	13	5	4	6	12	8	5	8	2	1	1	2	1	2	3	19
	C4		0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	C6		0	1	2	1	2	1	2	1	2	1	0	1	2	2	2	6	2	3	5	1	1
	C7		26	8	1	9	14	13	2	1	0	1	1	1	6	5	3	6	10	11	1	0	5
	C8		1	1	1	1	7	1	1	2	5	1	1	1	1	5	3	2	4	1	3	1	2
	C9		3	2	1	5	4	1	2	4	1	1	1	2	1	5	1	2	1	1	1	2	5
	C10		0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
	C11		0	0	0	0	2	0	0	1	1	1	1	1	1	1	0	0	0	0	1	1	1
	C12		0	1	0	1	1	1	0	1	1	0	0	1	0	1	1	7	1	0	0	0	3
	C15		6	2	7	7	11	0	3	3	3	3	7	0	2	1	3	1	1	1	3	4	1
	C18		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	C19		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	C21		1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	C22		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	C25		0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
	C27		7	8	6	14	20	26	2	12	6	8	8	11	18	2	6	6	11	11	17	15	10
	C29		0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
	C30		1	0	0	1	2	1	0	1	0	0	0	0	0	1	1	0	1	1	1	1	0
	C31		1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	C33		0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	C34		0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
	C35		1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
	C36		0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	C37		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Land-hopper	D1		339	79	164	140	72	183	172	94	141	136	140	73	91	111	149	127	93	67	76	60	34
Bugs	E1		1	0	1	0	1	1	0	1	1	1	1	1	0	1	0	1	0	0	1	1	1
	E2		1	0	1	1	1	0	1	1	1	0	1	0	0	1	1	0	1	0	1	1	1
	E4		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	E5		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	E7		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	E10		0	1	0	1	1	0	1	0	1	1	1	0	0	0	0	1	0	0	0	0	2
	E11		0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	E13		0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0
	E14		1	0	1	0	1	0	1	1	1	1	1	1	0	2	1	0	0	0	0	0	1
	E15		0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
	E16		0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0
	E17		0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Earwigs	F1		2	1	1	1	3	1	0	1	1	1	0	0	0	0	1	1	0	0	1	1	0
	F2		1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
	F3		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Crickets and Grasshoppers	G1		5	0	1	1	1	8	1	1	1	2	1	2	0	1	1	1	0	1	0	0	0
	G2		0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0
	G4		1	1	3	2	1	1	0	1	1	0	0	0	1	3	1	1	0	1	1	1	0
	G5		1	1	0	0	1	1	1	1	1	0	1	1	0	0	1	1	1	0	0	1	3
Mites and Ticks	H1		3	0	1	1	1	1	4	1	1	2	1	0	3	1	1	2	0	1	1	1	0
	H2		0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
	H3		0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
	H4		0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0
	H5		0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	H6		0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	H7		0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
	H9		0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	1	0	0	0	0	0
	H10		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	H11		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0

Morphospecies	Forest	A	A	A	A	A	A	B	B	B	B	B	B	C	C	C	D	D	D	E	E	E
	Quadrat	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	1	2	3	1	2	3
Cockroaches	I1	3	1	1	1	1	5	1	1	6	5	1	1	2	2	2	1	1	1	2	2	1
	I2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Wasps and Bees	K3	2	1	1	1	3	1	1	1	1	1	1	2	1	2	1	0	0	1	1	1	1
	K13	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
	K14	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0
	K15	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Spiders	L1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0
	L2	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
	L3	1	2	0	1	4	5	1	1	1	1	1	1	2	1	0	1	1	0	0	1	2
	L4	1	1	1	3	3	3	2	1	1	0	1	0	1	1	1	1	0	0	1	2	2
	L7	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
	L8	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
	L9	1	1	3	8	6	1	7	1	5	3	1	1	2	0	2	1	1	3	3	4	2
	L10	1	0	1	2	1	1	1	1	2	1	1	0	2	2	1	8	0	1	1	1	0
	L11	2	1	1	0	0	1	1	0	1	0	0	1	1	1	1	1	1	1	1	1	1
	L13	2	0	0	1	1	0	1	1	0	0	1	1	0	0	0	0	0	0	1	1	0
	L14	1	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	L15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
	L16	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0
	L17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
	L18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
	L19	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0
	L20	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
	L21	0	0	0	0	0	0	0	1	1	1	1	1	1	0	1	0	0	0	0	0	0
	L22	1	1	1	5	1	1	1	1	1	1	1	1	0	0	0	1	1	0	1	1	1
	L23	1	0	0	0	1	0	1	1	1	1	1	1	0	0	0	0	0	0	1	1	1
	L24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Centipedes	M1	3	1	8	5	5	2	8	4	3	3	2	1	0	3	2	2	1	1	1	1	3
	M2	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0
	M3	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
	M4	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
	M5	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
	M6	0	0	1	1	0	1	0	0	0	0	1	1	2	1	1	0	0	0	0	0	0
Millipedes	N1	3	1	4	8	6	1	2	3	1	5	1	1	2	3	1	2	1	2	3	1	1
	N2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0
	N4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
	N5	1	1	0	0	1	1	1	0	1	0	0	1	1	0	1	1	1	0	1	0	0
	N6	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0
	N7	1	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0
Woodlice	O1	12	1	7	1	1	3	7	5	5	7	4	2	2	4	1	3	1	6	3	2	1
	O2	0	0	0	0	1	0	1	1	0	1	1	0	1	0	0	0	1	0	0	0	0
	O3	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
Pseudoscorpions	Q1	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0
Archaeognaths	T1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 3. Abundance (no. of individuals) of morphospecies identified in forests of the Balgowan complex.

		Balgowan complex (grassland matrix)																			
Morphospecies	Forest	A	A	A	A	A	A	B	B	B	B	B	B	C	C	C	D	D	D	E	E	E
	Quadrat	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	1	2	3	1	2	3
Ants	A1	37	37	32	48	42	27	22	13	8	17	21	23	44	27	15	54	17	34	42	18	13
	A2	1	0	1	1	1	1	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0
	A3	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	A4	1	1	1	1	1	1	9	4	1	2	4	2	1	0	1	0	1	1	1	1	0
	A5	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0
	A6	1	1	0	1	0	0	1	2	1	1	1	1	1	9	4	1	0	0	0	0	1
	A7	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
	A8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	A9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	A10	0	1	1	1	1	0	0	0	0	0	0	0	0	1	1	1	1	0	1	0	1
	A12	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	A13	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0
Beetles	B1	26	23	12	20	22	19	9	6	11	7	8	10	28	17	13	44	11	32	36	22	25
	B2	1	2	1	1	1	1	1	1	1	1	3	3	2	1	4	1	3	5	2	4	2
	B3	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	B4	0	0	0	0	1	0	1	1	1	0	1	1	1	0	0	0	0	0	1	0	1
	B5	6	1	1	1	2	1	8	7	4	13	13	7	20	10	2	8	4	12	4	9	5
	B6	6	1	1	1	9	1	20	21	22	22	22	16	13	11	16	4	8	9	15	8	7
	B7	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
	B8	2	3	1	1	4	1	2	1	4	2	1	1	8	1	2	4	2	9	6	5	4
	B9	3	13	6	11	13	7	2	3	2	2	3	1	1	1	1	11	4	14	14	5	9
	B10	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
	B11	1	1	1	1	1	1	1	4	7	4	1	2	2	1	1	0	1	2	1	0	0
	B12	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0
	B13	1	1	1	0	1	1	4	7	1	11	5	5	0	0	0	0	0	0	0	0	1
	B15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
	B16	0	1	1	0	1	1	3	2	2	2	2	1	1	2	1	1	22	1	2	1	16
	B17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	B18	1	0	1	1	1	0	1	1	1	1	2	0	6	0	1	1	1	1	1	1	1
	B19	1	1	1	2	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
	B21	1	5	2	3	6	3	2	1	2	7	5	1	16	2	1	1	1	6	4	1	6
	B22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	B23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
	B24	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0
	B25	0	0	1	1	0	1	1	1	0	0	1	1	0	0	0	0	0	0	1	0	0
	B26	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	B27	0	1	0	0	0	1	0	0	0	1	1	1	0	0	0	0	0	1	1	0	0
	B28	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
	B30	1	0	0	0	0	0	1	1	1	2	1	1	0	0	0	0	0	0	0	0	0
	B33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	B35	0	1	0	0	1	0	0	1	1	1	0	1	0	1	1	0	0	1	0	0	0
	B36	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0
	B37	2	1	1	2	1	1	1	2	1	1	1	1	1	1	1	1	1	1	3	1	0
	B38	1	1	1	1	1	1	3	1	3	5	3	1	1	0	0	0	1	1	0	0	1
	B39	1	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
	B40	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	B41	0	1	0	0	0	0	2	0	1	1	2	1	0	1	1	0	1	0	0	0	0
	B42	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
	B43	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
	B44	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	0	0	0
	B45	0	1	1	1	2	0	0	0	0	0	0	0	1	1	0	1	1	1	1	1	0
	B46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	B47	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0
	B48	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0
	B49	1	0	0	1	0	0	0	1	1	0	0	0	1	1	1	1	1	1	0	0	0
	B50	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	B52	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
	B54	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
	B55	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0
	B56	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	B57	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
	B58	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
	B59	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
	B60	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	B61	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
	B62	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
	B63	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	B64	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 3 cont.

Morphospecies		Forest	A	A	A	A	A	A	B	B	B	B	B	B	C	C	C	D	D	D	E	E	E
														Balgowan complex (grassland matrix)										
		Quadrat	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	1	2	3	1	2	3
Flies	C1		15	8	5	2	6	5	3	4	1	2	4	9	7	6	5	17	7	10	21	8	6
	C2		4	15	15	5	7	3	2	1	2	2	3	1	1	2	3	2	1	7	3	1	3
	C3		4	25	22	18	18	31	3	3	1	3	5	2	2	1	1	1	6	5	3	1	5
	C4		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	C6		1	1	1	1	1	1	1	1	1	1	2	2	1	3	3	1	1	5	1	2	2
	C7		2	3	1	3	4	2	3	5	3	2	1	4	1	1	1	8	1	7	3	1	1
	C8		1	1	3	1	3	1	1	2	1	2	3	1	1	2	5	2	1	3	3	1	0
	C9		1	2	1	1	3	6	3	3	1	2	1	2	2	2	5	1	4	5	2	2	1
	C10		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	C11		1	0	1	1	0	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1
	C12		0	0	0	1	1	1	0	1	1	1	0	0	0	1	1	1	1	1	2	0	1
	C15		3	3	3	2	9	1	5	2	3	1	1	0	2	1	5	7	1	5	4	5	2
	C18		0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	C19		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	C21		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	C22		0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
	C25		0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
	C27		9	13	4	1	1	3	7	14	13	11	23	15	1	1	3	21	11	18	2	8	10
	C29		0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	C30		1	0	1	1	0	0	1	1	0	1	1	0	0	1	0	3	2	1	0	3	1
	C31		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	C33		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
	C34		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	C35		1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	C36		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	C37		0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Land-hopper	D1		72	20	30	18	55	39	34	51	9	29	64	49	65	125	73	146	76	87	344	86	61
Bugs	E1		1	1	1	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0
	E2		1	1	1	1	1	0	1	4	1	1	1	1	0	0	1	0	0	1	1	0	1
	E4		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	E5		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	E7		0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
	E10		0	1	0	0	2	0	1	1	0	2	1	0	0	0	1	0	0	1	2	1	0
	E11		1	1	1	1	1	1	1	1	1	1	0	1	1	0	0	0	0	0	0	0	4
	E13		0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
	E14		1	0	0	1	1	1	1	1	0	1	1	1	1	1	0	1	1	0	1	1	1
	E15		0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	E16		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	E17		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Earwigs	F1		1	0	1	1	1	1	0	1	1	1	0	0	1	1	1	0	1	1	0	0	0
	F2		0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
	F3		1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Crickets and Grasshoppers	G1		1	0	3	1	1	0	1	0	0	0	0	0	0	0	0	1	0	0	1	1	0
	G2		0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2
	G4		1	0	1	2	1	1	1	1	1	1	1	1	1	1	1	0	1	2	1	1	0
	G5		0	0	1	0	0	1	1	1	1	1	1	1	0	0	0	1	0	1	1	0	0
Mites and Ticks	H1		1	1	1	1	1	0	0	0	0	0	0	1	6	1	1	1	1	2	1	5	4
	H2		0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1
	H3		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	H4		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	H5		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	H6		0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
	H7		1	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	1	0
	H9		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	H10		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	H11		2	1	1	0	0	1	1	0	1	0	0	1	1	0	0	0	1	0	0	0	0

Morphospecies		Forest	A	A	A	A	A	A	B	B	B	B	B	B	C	C	C	D	D	D	E	E	E
		Quadrat	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	1	2	3	1	2	3
Cockroaches	I1		3	2	0	3	3	2	1	1	2	0	1	1	4	1	1	0	2	1	10	2	4
	I2		0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Wasps and Bees	K3		1	2	1	1	1	1	1	1	0	1	0	0	1	1	1	0	1	1	1	0	1
	K13		0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0
	K14		0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	1	0	1	1	0
	K15		0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Spiders	L1		0	0	0	1	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
	L2		0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
	L3		1	0	0	0	0	1	1	1	0	1	1	1	1	2	1	1	1	1	0	1	1
	L4		1	0	0	0	0	1	1	0	0	1	0	1	2	1	0	0	0	1	1	1	3
	L7		0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1
	L8		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	L9		1	1	2	1	5	1	3	1	2	1	1	1	3	4	4	1	8	5	1	2	4
	L10		1	1	1	1	2	1	1	1	1	1	2	1	1	1	3	1	1	2	4	1	4
	L11		1	1	1	1	1	0	1	1	1	1	1	0	0	2	2	0	1	1	1	0	2
	L13		1	1	0	1	1	0	0	1	1	1	0	0	0	1	1	0	0	1	1	0	0
	L14		1	0	0	0	0	1	0	0	0	0	0	0	1	1	1	0	0	0	1	1	0
	L15		0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
	L16		0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
	L17		0	0	U	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	L18		0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
	L19		0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
	L20		0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0
	L21		0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
	L22		1	1	1	0	0	0	1	1	1	0	1	1	1	1	2	0	1	4	0	1	1
	L23		0	0	0	0	1	1	0	1	1	1	1	1	1	0	1	1	0	0	0	0	1
	L24		0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Centipedes	M1		1	0	0	0	3	1	1	1	1	2	1	1	4	4	1	2	1	7	2	3	4
	M2		0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0
	M3		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	M4		0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0
	M5		0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	M6		1	1	0	1	0	0	1	0	1	1	0	0	0	0	0	0	0	0	1	0	1
Millipedes	N1		1	1	2	1	3	1	8	3	20	3	2	1	8	1	1	2	2	1	4	3	7
	N2		0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
	N4		0	0	0	1	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	1	1
	N5		0	1	0	3	1	0	0	0	0	0	1	1	2	1	1	0	1	1	0	0	0
	N6		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	N7		0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0
Woodlice	O1		4	1	1	3	1	2	7	3	4	3	3	1	8	3	6	5	43	33	19	5	11
	O2		0	0	1	0	0	0	0	0	0	0	3	0	1	1	1	0	10	1	1	1	17
	O3		0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Pseudoscorpions	Q1		0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	1
Archaeognaths	T1		0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0

Balgowan complex (grassland matrix)