Webs, mandibles and capsules - Is mapped vegetation type a surrogate for beetle and spider assemblages?

by

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Declaration

This thesis contains no material which has been accepted for the award of any other degree or diploma in any tertiary institution, and to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference is made in the text of the thesis.

Signed

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During the process of reducing memory and conversion to pdf in order to make this thesis available electronically on the web, some formatting errors occurred, particularly in the results chapter. Apologies.

Abstract

Increasingly, the effectiveness of surrogate species as a management tool for reservation of biodiversity has been questioned. It has been established that mammal and bird distributions correspond to vegetation type, but for invertebrate species this is less clear. This assumption was tested by comparing the communities of species of two invertebrate taxa in forest litter, spiders and beetles with pitfall sampling. Sampling occurred in spring summer and autumn in the foothills of Mount Wellington in 2002 and 2003 within 6 different adjacent eucalypt forest types - *Eucalyptus regnans* forest (WRE), *E. obliqua* with broadleaf shrubs (WOB), *E. obliqua* dry forest (DOB), *E. tenuiramis* forest on sediments (DTE), *E. amygdalina* forest on mudstone (DAM) and *E. pulchella* forest (DPU).

The total number of beetles collected was 1726, representing 152 species from 28 families. Spiders totalled 1983 representing 204 species from 20 families. A third of these were juveniles and data were analysed separately with and without the juveniles. Forest type was a significant factor affecting distribution of spiders and beetles but was different for different forest types.

There was a significantly different spider community in wet WOB while communities in WRE and dry DOB overlapped suggesting change along a continuum from wet to dry forest. Species responsible were vagrant hunters from the families Corrinidae, Gnaphosidae, Lycosidae, Zodariidae, Zoridae and a Micropholcommatidae web builder. Beetles were also significantly different between dry *E. tenuiramis* (DTO) and *E. amygdalina* (DAM) and a wet WRE-WOB-DOB continuum was detected. Species responsible for this separation were *Isopteron obscurum* (Erichson, 1842): Tenebrionidae, *Tetrabothrus claviger* (Fauvel, 1878): Staphylinidae and some fungivores - *Nemadini* (Leiodidae), *Scaphidium* sp.: Staphylinidae, *Thalycrodes australe* (Germar, 1848): Nitidulae, and *Acrotrichis* sp.: Ptilidae.

A total of 56 soil, topographic, ground cover, microclimate and vegetation variables were measured. Their significance for predicting the distributions of spiders and beetles better than vegetation alone was examined. Statistical analysis revealed environmental gradients along which beetles and spiders were dispersed. Beetles were distributed along a moisture and a ground cover gradient. Spiders were separated along a soil nutrient and a moisture/temperature gradient. These gradients varied among sites in the same forest type as well as among sites in different forest types, and explained some of the site scale variation in assemblages.

At a larger geographic scale, sampling at 36 sites grouped into 3 regions in southeastern Tasmania: Hobart, Levendale and Swansea, tested assemblage differences across a span of 157 km. Beta diversity was highest at the scale of 50 km. This is suggested as the maximum distance that should separate patches of the same forest type in order to capture maximum spatial variation in diversity of beetles and spiders across a vegetation based reserve mosaic. The research highlights the complexity of invertebrate interactions with forest type and environmental variables and indicates that simple prescriptions which can inform planning of reserves are not readily obtainable from examination of assemblages as a whole.

Theridiidae

Segestriidae

Zodariidae

Zodariidae

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Preface

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Lucanidae

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Introduction

Policy context of biological diversity: global to local

Arising from the Earth Summit in Rio de Janeiro in 1992 Australia ratified the Convention on Biological Diversity in 1993 (Commonwealth of Australia, 1995) and committed itself to conservation of biological diversity. Soon after, Australia became part of the Montreal Process which is a working group that establishes and implements a framework of criteria and indicators for assessing sustainable management and conservation of temperate and boreal forests. It was formed in 1994 and membership countries cover 90% of the world's temperate and boreal forests (Montreal Process Working Group, 1995). The indicators were endorsed as voluntary guidelines for policy makers under the Santiago Declaration in the ten member countries - Australia, Canada, Chile, China, Japan, Republic of Korea, Mexico, New Zealand, Russian Federation and United States of America.

Biological diversity is one of seven criteria in the Montreal Process and three components have been identified for its assessment: ecosystem, species and genetic diversity. Species diversity, which is measured by the number of forest dependent species and their reservation status (Montreal Process Working Group 1995), has largely focused on plant species; and ecosystem diversity has been characterised by forest type (Montreal Process Working Group, 1995). Thus vegetation type and diversity have become default measures of diversity due to lack of extensive, comprehensive surveys of other taxa. In Tasmania recent research (Baker 2006; Baker *et al*. 2007; Grove and Yaxley 2005; Michaels and McQuillan 1995) has contributed to a body of knowledge about forest dependent beetles which are becoming identifiable as indicator species that could be incorporated into biological diversity assessments in the State.

The National Strategy for Ecologically Sustainable Development (Commonwealth of

Australia, 1992) arose from international obligations under Agenda 21 (UNCED, 1992) and provides directions for Australian policy making to conserve biological diversity as one component of ecologically sustainable development. Progress in ecologically sustainable development is reported through State of the Environment Reporting where there have been efforts to identify suites of biologically and ecologically representative and sensitive taxa to which a pressure/condition/response model can be applied for planning (Saunders *et al*. 1998).

Commonwealth protection of biodiversity is now facilitated through the National Strategy for the Conservation of Australia's Biological Diversity (Department of Environment, Sports and Territories 1996). The strategy's objectives include identification of ecosystems and threatening processes, species and subspecific variation, bioregional planning and management, conservation management, establishment of a comprehensive, adequate and representative system of protected areas (the CAR system), improving biological diversity conservation outside reserves, and recognition of the ethnobiological knowledge of indigenous people. Within this framework the Interim Biogeographic Regionalisation for Australia (IBRA) (Environment Australia, 2000) provides a landscape-based approach to mapping ecosystems across Australia resulting in biotic and abiotic information for conservation of biodiversity instead of solely vegetation data.

Bioregions (Figure 0.1) are based on mapped environmental attributes rather than raw data, since these attributes are reflected by flora and fauna patterns of distribution (Thackway and Cresswell 1995). In Tasmania regions are grouped by their similarity in landform, geology/lithology, climate, vegetation and floristics (Environment Australia 2000) and build upon Orchard's 13 biogeographical regions (including Macquarie Island) for herbarium records (Orchard, 1988), in use since 1982. In the mid 1980s the Tasmanian Forestry Commission modified the Hebarium regions slightly and adopted 11 Nature Conservation Regions (including Macquarie Island) by removing Mt Field and Mt Wellington as separate regions (Orchard 1988).

As reports by the IBRA point out (Thackway and Cresswell 1995), IBRA provides a guide for identifying gaps in our National reserve system, but is not a basis for reservation of particular land parcels. The IBRA can assist planning to fill gaps in the reserve system based on comprehensiveness and representativeness but does not assist with the third CAR criteria of adequacy, a criteria which needs to be explored at a finer scale and should include variables outside the scope of the IBRA such as the level of threat to biodiversity (Thackway and Cresswell 1995). Comprehensiveness is the degree to which the full range of ecological communities and their biological diversity are incorporated in the reserve system (RPDC 2003).

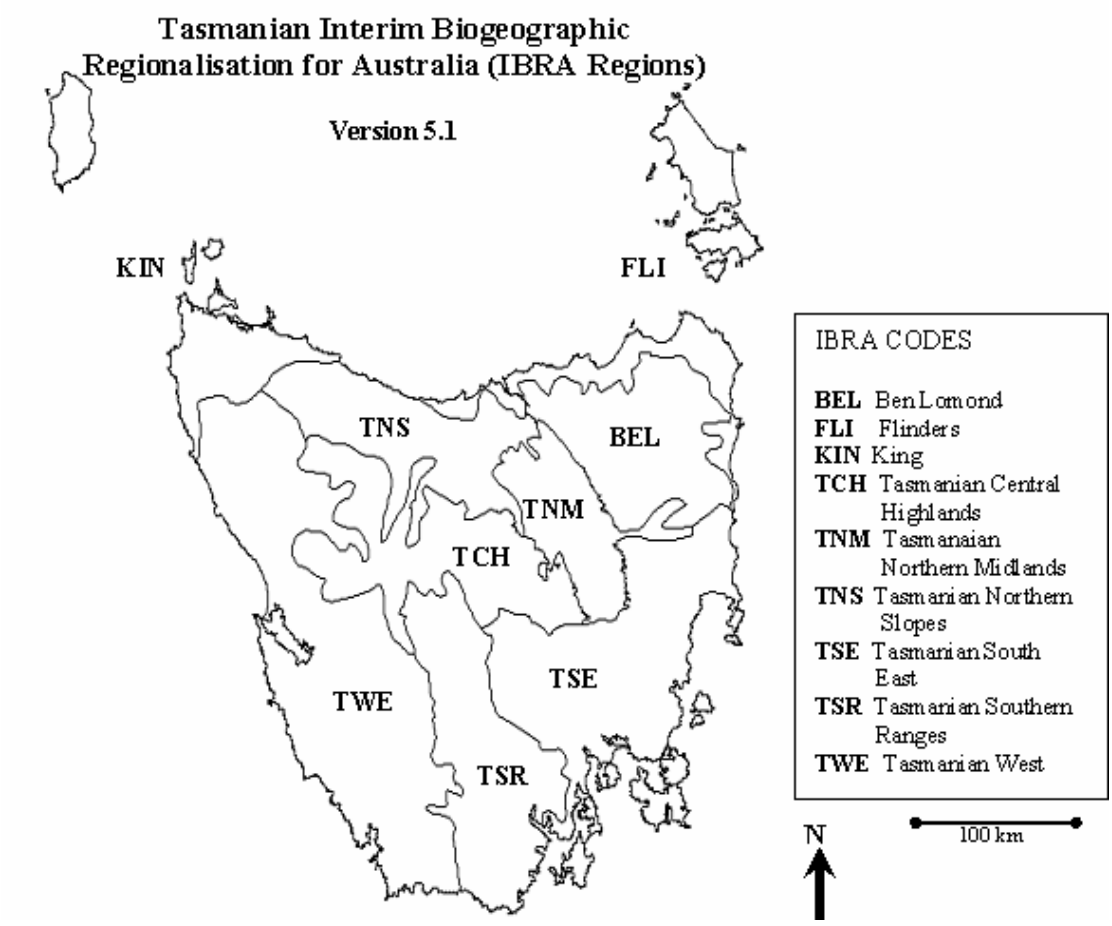


Figure 0.1 Map of Tasmanian Interim Biogeographic Regionalisation for Australia (IBRA Regions) displaying Tasmania's nine bioregions. The map is based on information from http://www.deh.gov.au/parks/nrs/ibra/version5-1/tas.html

In Tasmania conservation of biodiversity is managed by reserving different vegetation types. The underlying assumption that the distribution of other species follows that of vegetation type (Panzer and Schwartz 1998; Scott *et al*. 1993) has been questioned

(Ferrier *et al*. 1999; Mesibov 1993; Oliver *et al*. 1998; York 1999). Vegetation type is a commonly selected surrogate for all biodiversity because it is relatively easy to map from aerial photos compared with comprehensive on-ground surveys of the distribution of a variety of vertebrate and invertebrate species in several taxa.

Under the 1997 Tasmanian RFA (Regional Forestry Agreement) biodiversity is reserved through reservation of representative vegetation types of which 50 different types have been mapped (Harris and Kitchener 2005).

While several studies show that the distribution of mammals and birds have distribution patterns which follow vegetation types (French, 1999), the same is not true for invertebrates such as carabid beetles (Michaels 1999), and a study in Tasmanian rainforests demonstrated that a distinct invertebrate rainforest fauna was not identifiable (Mesibov 1993). Studies in other parts of Australia have also found poor congruence between invertebrate assemblages and forest types (Oliver *et al*. 1998) or remnant size (Major *et al*. 1999; Gibb and Hochuli 2002). Assemblages in small fragments of a forest type are not a subset of species found in larger fragments, being instead, entirely different (Major *et al*. 1999; Gibb and Hochuli,\ 2002) or intermediate between continuous native vegetation and wildlife strips (Grove and Yaxley 2005); again indicating that vegetation type is not the primary factor influencing invertebrate assemblages (Coy *et al*. 1993). Hypothetical reserves based on surrogate species have been found to be no more effective in protecting overall species richness than reserves based upon a random suite of species (Andelman and Fagan 2000). It has been demonstrated that selection of the largest patches of habitat can perform almost as well as a data-intensive search for indicator species (Podani *et al*. 1997); while Araujo *et al.* (2001), found that the representation of species by environmental diversity was not significantly different from the level obtained by selecting the same number of areas randomly. '*Given the numerical dominance of invertebrates, it is not surprising that the efficacy of basing acquisition decisions primarily on plant criteria is being questioned*,'(Panzer and Schwartz 1998, p. 694).

The influence on invertebrates of many factors including litter depth (Michaels and McQuillan 1995; York 1999), disturbance history (Mossakowski *et al.* 1990), geographical distance (Oliver *et al*. 1998), microclimate, organic matter and physical

and geographical features (Ferreira and Silva 2001) have been recognised and considered to be better predictors of invertebrate abundance than vegetation type (Mesibov 1993). Others have demonstrated that invertebrates do not respond to forest type but variation in the structure of vegetation (Coy *et al.* 1993; Greenslade and New 1991; York 1999), biochemical properties of plants and genetic variation within plant species (Bangert *et al*. 2006; Dungey *et al*. 2000). For this reason a large number of environmental variables have been measured during this research to identify variables that might provide better surrogate measures for invertebrates.

The research is significant because reservation of biodiversity in Tasmania is largely based on vegetation type since it is easier to map yet it is not known to what extent vegetation as a surrogate adequately reserves invertebrate diversity. To do this, spider and beetle assemblages were not only examined at a small scale in an intensive study at a local set of adjacent sites, but were compared at a larger scale at three locations (Hobart, Levendale and Swansea) within the bioregion of Eastern Tasmania.

Knowledge about invertebrates gained from this study will contribute to use of invertebrates to monitor the health of different vegetation types for the protection of biodiversity which is threatened by human impacts. Invertebrates respond quickly to changes in their environment and are increasingly being used as indicators of impacts on ecosystems of permissable human activities such as grazing and fire (Harris *et al*. 2003), firewood collection (ANZECC 2001), timber harvesting (Baker *et al*. 2007) and silviculture (Michaels and McQuillan 1995) within, or adjacent to, reserved vegetation types. Invertebrate monitoring can provide a valuable tool for monitoring sustainable management and protection of Tasmania's variety of vegetation types. It is also expected that the results of this study may contribute to refining an appropriate suite of surrogate species which could be representative of invertebrate biodiversity in Tasmania and contribute to the debate on the effectiveness of surrogacy in conservation management.

RESEARCH QUESTION:

The broader scope of this thesis addresses the topical question whether vegetation type is an appropriate surrogate for invertebrate biodiversity. My specific test of this question focuses on two biodiverse invertebrate groups, spiders and beetles, and their distribution in relation to six different types of eucalypt forests in south eastern Tasmania.

RESEARCH OBJECTIVES

My research objectives cover descriptive, analytical and predictive aspects, as follows:

(i) To describe the assemblages of spiders and beetles present in six different eucalypt forest types and a range of environmental variables.

(ii) To examine whether the assemblages of spiders and beetles differ at each of six eucalypt forest types and whether certain taxa are indicative of those habitats or their environmental attributes.

(iii) To investigate to what extent characteristic species assemblages can be proposed for each forest type.

(iv) To examine which environmental variables are significant for particular spider or beetle assemblages and whether these variables predict the species composition of assemblages better than vegetation alone.

(v) To consider the scale at which variables influence assemblages of spiders and beetles by comparing assemblages at two scales: an intensive scale (24 sites within 2 km^2), and an extensive scale (three locations spanning approximately 157 km from Pelverata, Hobart, through Levendale to Hardings Falls, Swansea.

(vi) To what extent is spatial autocorrelation among sites, taxa and environmental variables a significant predictor of community composition?

A question that then emerges from the analysis which has implications for the conservation management of invertebrate communities.

(vii) What, therefore, is a biologically meaningful scale at which to sample and manage invertebrate diversity?

Thesis Outline

Following on from the policy background provided in the Introduction, Chapter 1 provides a literature review of the current debate on the adequacy of vegetation as a surrogate for biodiversity. A review of previous studies of invertebrates in Tasmania and Australia is followed by a discussion of the way in which species diversity has become a measure of biodiversity.

Experimental design, methodology and statistical analyses selected for this research are presented in Chapter 2, with results detailed in Chapter 3. Chapter 4 focuses on discussion of the results. Chapter 5 discusses the implications of the results for planning in the field of biodiversity.

An essential but invisible part of the work undertaken during this study was to provide a secure taxonomic foundation for the project. A refence on identification of Tasmanian weevils (Curculionidae) and ground beetles (Carabidae) was developed to enable identification of species and morphospecies. It was a time consuming task to draft mock keys for local species, locate original descriptions of species from 100 years ago, and photograph specimens. It appears I was not alone in experiencing difficulties with unravelling the subtleties of identification, as Thompson (1992, p. 834) comments: '*Classification of weevils is like a mirage in that their wonderful variety of form and the apparent distinctiveness of many major groups lead one to suppose that classifying them will be fairly straightforward but, when examined closely, the distinctions disappear in a welter of exceptions and transformation series*.' However, accuracy in identification is central to providing meaningful data for analysis, if identified indicator species are to be used by many workers in the biodiversity field. Names of species also unlock storehouses of information about them (Zimmerman 1994, p. 34).

Chapter 5 Background

'*Patterns of biodiversity will necessarily be complex and variable'* (Underwood and Chapman 1999).

4.1 Species diversity as a measure of biodiversity

Ecosystem diversity, containing habitats, species and processes (Doherty *et al*. 2000) is notoriously difficult to quantify and is often erroneously reduced to a functional assessment of 'physical habitat with an associated assemblage of interacting organisms' (Noss, 1996) or even habitat diversity alone (Faith and Walker, 1996).

Habitat diversity as a measure of biodiversity is also difficult to quantify because of difficulty in defining boundaries, and measuring physical structure and vegetation consistently at appropriate scales for the species that the habitat is defined as supporting (Christensen *et al.* 1996; Southwood 1978).

Species diversity provides a quantifiable measure of biodiversity and functional roles. Extrapolation from one or two species or taxa to biodiversity hinges upon selection of surrogate species. Measures of biodiversity include species diversity and species richness. Species richness (S or SR) is the additive sum of the species in a sample or habitat while species diversity considers both the SR and various measures such as eveness as measured by a variety of indices. Both measures have been used in a number of Australian studies (Churchill and Arthur 1999; Lindenmayer *et al*. 2000; MacNally *et al*. 2002; Oliver *et al*. 1998; New 1999).

4.1 The adequacy of vegetation type as a surrogate for biodiversity reservation

Fleishman *et al*. (2001) define surrogate species as those that provide a scientifically reliable and cost-effective substitute measure of other ecological variables.

The question of whether vegetation type can serve as an adequate surrogate for biodiversity more generally has gained some recent attention especially in relation to land use change. The use of plant species diversity as a surrogate for biodiversity is supported by Scott *et al.* (1993) in their study of GAP analysis where species or communities that are not protected are identified. At a coarse scale vegetation measures may indeed be reasonable indicators for invertebrates. In north American prairies near Chicago, native plant species richness explained 28% to 49% of invertebrate species richness (Panzer and Schwartz, 1998), but vegetation type as surrogate for biodiversity remains to be tested adequately in Australia.

Since 1995 much of Tasmania's protection of forest biodiversity has been mediated through the prescriptions of the Regional Forest Agreement (RFA) and its amendments (DPAC 2003) where biodiversity reservation is based on forest type as a surrogate to meet the requirements of a Comprehensive, Adequate and Representative (CAR) set of protected areas. This approach implies that patterns of distribution of a variety of species vary systematically in relation to vegetation type, an approach that is still current policy in Tasmania.

The same question of surrogacy can be asked at other levels within natural communities. For example, among invertebrates, are spiders and beetles effective surrogates for broader invertebrate biodiversity or even each other? Is there congruence between invertebrates and the local vegetation? If not, how might the more familiar vegetation reservation model be modified to allow for this?

As Faith *et al*. (2003, p. 9) ask, '*what constitutes good evidence for an effective biodiversity surrogate*?' There is evidence that invertebrate density is related to non-forest-type parameters such as vegetation structure (Lawton 1983; Lawton and Shroder 1977; Strong and Levin 1979), disturbance history of the ground layer (York 1999; Gibb and Hochuli 2002), and biochemical properties (Bernays and Chapman

1994; Connor *et al*. 1980; Fowler and Lawton 1982; Niemela and Mattson 1996). Even where differences in inveterbrate assemblages have been found between vegetation types it has been observed that the differences may be due to other factors. For example differences in assemblages in pine plantations compared with eucalypt plantations were attributable to differences in forest management where increased coarse woody debris from prunings and thinnings in pine planations provided a different habitat for invertebrates compared with mound ploughing in eucalypt plantations which increases leaf and twig litter (Bonham *et al*. 2002). Thus vegetation-type alone may not be an adequate indicator of biodiversity (Mesibov 1993; Ferrier *et al*. 1999; Gibb and Hochuli 2002).

A functional definition of biodiversity as a process (Faith *et al*. 2003) rather than simply a compositional inventory of species, genes, etc. has been adopted for the purposes of this research. The purpose is to identify species as indicators of the heterogeneity (Sarkar and Margules 2002) of ecosystems in order to increase the valuing of ecosystem processes, rather than a list of species *per se*. This poses challenges for applying a traditional compositional analysis of data, with its focus on quantifiable measures of number of species etc, within a more holistic functional approach which can build upon our understanding of sustainable ecosystems.

4.2.1 Invertebrates as surrogates for biodiversity

The biogeography of Tasmania reflects the complex topography, local climates and biological diversity of the island. For invertebrates this complexity is especially influential. Whereas the IBRA (Environment Australia, 2000) recognises 9 terrestrial bioregions based upon vertebrates, floristics and environmental data, Mesibov (1997) identified 24 invertebrate bioregions in Tasmania and noted that they were not congruent with any mapped geological, geomorphological, vegetation or vertebrate distributions.

Various taxa might serve as useful indicators depending on a number of criteria. Coy *et al.* (1993) recommended springtails (Collembola) as showing promise as an indicator group in Tasmanian rainforests because they are abundant and species rich, yet manageable (about 100 species). Mites (Acarina) although rich in species are, at

present, too little known taxonomically. Coy *et al*. (1993) argue that Coleoptera, on the other hand, are too species rich, not all well enough known taxonomically, and usually include a high number of singletons, though they concede that some individual Coleoptera families may be useful indicators. Carabid beetles have a considerable history of use in this regard elsewhere (Cole *et al*. 2005; Davies and Margules 1998; Michaels 1997 and 1999; Michaels and McQuillan 1995; Niemala *et al*. 1992). Litter invertebrates such as Opilionida, Isopoda and Amphipoda are better known taxonomically but have too few species in Tasmania, comprising less than 20 species each, to be sensitive indicators.

Tasmanian spiders have been surveyed in coastal heathland (Churchill 1993), and temperate rainforests (Coy *et al*. 1993) and wet eucalypt forests (Robertson 1994). While spiders are not well known taxonomically, the resolution of data produces similar results if morphospecies (Derraik *et al.* 2002; Oliver and Beattie 1993; Pik *et al.* 1999) or, perhaps more correctly, parataxonomic units (Krell 2004; Majka 2006) are identified.

In the wider Australian context, beetles spiders and ants (Gibb and Hochuli 2002; Harris *et al.* 2003; Major *et al*. 1999; Oliver and Beattie 1996 and Oliver *et al*. 1998) have featured as potential indicators of invertebrate biodiversity. Litter spiders and beetles are relatively easy to sample, are sensitive to changes in ecosystems such as vegetation structure (Thiele 1977; Uetz 1991) and occupy identifiable functional roles in ecosystems (Springett 1978; Wise 1993). Beetles and spiders were therefore selected for this study as an adjunct to a concurrent ant survey from the same samples (Meeson 2006).

4.2.1 Environmental variables that show promise as factors that are responsible for the variation in distribution of beetles and spiders.

Large scale environmental variables do not necessarily enable prediction of invertebrate assemblages (Underwood and Chapman, 1999) and Tasmania's complexity makes it '*unwise to assume that invertebrate species are distributed more than a few km from known localities*' (Mesibov, 1994, p. 136). Small scale differences such as microclimate, disturbance and presence of other invertebrate species can affect an assemblage (Gibb and Hochuli, 2002; Mesibov 1994; Underwood and Chapman 1999). At the same time, it is recognised that species distributions are influenced at a larger regional scale by factors such as temperature which might limit distribution of a species, even if suitable site-scale factors exist (Eyre 2006).

At a finer scale, a number of relationships have been determined between plant and soil nutrients and beetles. A number of eucalypts have adapted to low phosphorus and nitrogen levels in soil, while other plant families such as *Acacia*, *Pultenaea* and *Daviesia* (legumes) and *Casuarina* have adapted through a symbiotic relationship with nitrogen-fixing bacteria (Williams 1991). Nitrogen and phosphorus concentrations are higher in wet sclerophyll forests than dry sclerophyll forest due to chemicals in leaves from trees of the mesophytic understory such as *Pomaderris* (high calcium and pH), *Olearia* and *Acacia* (Wells and Hickey 1999). Soil nitrogen concentration which can account for 50% of the variation total plant species richness (Le Broque and Bucksney 2003) contributes to the nitrogen in the phloem of trees. This has been shown to vary at a small scales of metres, from tree to tree and this has been found to influence presence of bark beetles such as *Dendroctonous frontalis* that feeds on phloem (Ayres *et al.* 2000). Phosphorus, on the other hand, is an example of a nutrient that varies at a much larger spatial scale of kilometres (Ayres *et al*. 2000) and therefore would be a less useful variable to measure for a study area of 200 square metres. Organic soil horizons provide a stable environment for litter dwelling species by providing a continuous food supply (McColl 1982). New Zealand *Nothofagus* litter is habitat for a Staphylinid beetle of the genus *Holotrochus* which is a close relative of

Typhlobledius sp. in Tasmania. The New Zealand beetle is used as an indicator of depth of organic horizon (McColl 1982).

Chemical changes during litter decomposition influence populations of detritivore species. Some detritivore populations increase with low C:N (carbon to nitrogen) ratios and low concentrations of polyphenolics (Satchell and Low 1967). The ratio of C:N indicates the availability of nutrients from decomposition and is high in forest litter where it can be >25. In soil C:N of 12-16 is typical of humus (Rayment and Higginson, 1992). Major chemicals in leaf litter include lignin, tannin, cellulose, hemicellulose, nitrogen and carbon which are altered by the action of microbi-detritivores such as springtails (Collembola). Indirect ecological relationships between beetles and nutrients have also been observed such as the finding that absence of ant and beetle predators in deciduous forests influences litter chemistry by decreasing litter decomposition (Lawrence and Wise 2004) or increasing its rate (Hunter *et al*. 2003). There seems to be a fine balance in the ratio of predators and collembola. A very low number of predators can reduce the decomposition of litter if there is a large increase in collembola which overgraze fungi that decompose litter (Lawrence and Wise 2004).

Pselaphidae and Scydmaenidae beetles are harmed by exposure to ultraviolet light from direct sunlight (Kuhnelt 1976) while a correlation between temperature and carabid activity (Greenslade 1964; Magura 2002) provides one example that temperature may be a variable in presence/absence of certain arthropods in litter fauna. High surface temperatures may coagulate body proteins, increase oxygen requirements and damage respiratory enzymes so soil fauna may seek subsurface soil depths. Sub surface soil temperatures are known to fluctuate less than at the surface (Kuhnelt 1976). Soil fauna may also seek moist soils since they are less subject to temperature fluctuations than dry soils due to a higher specific heat and are cooled by evaporation of capillary water that reaches the surface (Kuhnelt 1976). Moist soils in open areas would be avoided since once heated, they cool more slowly as

condensation of water vapour releases latent heat (Kuhnelt 1976).

Soil moisture and temperature are known to influence the distribution of carabid beetles (Judas *et al*. 2002; Thiele 1977) however the importance of these variables for other coleoptera species has been little studied (Niemela *et al*. 1992). Soil fauna varies in its response to duration and level of moisture. Ants and beetles, including elaterid and cockchafer larvae, are examples of 'unwettable' creatures that trap air bubbles in body hairs for respiration during inundation of soil. Soil fauna existing in drier relative humidities below 100% have characteristically stiff, club-shaped bristles to prevent dehydration through body contact with dry soil, and lay eggs on stalks (Kuhnelt 1976). Soil moisture level influences the diet of some species such as elaterid larvae that feed on humus in permanently wet soil but feed on roots and plants in dry soil (Kuhnelt 1976). Eggs of *Aphodius tasmaniae* Hope (Scarabaeidae) require a pF range (water holding capacity) of 2.50-3.75 in order to absorb water and hatch; and during the first instar do not extend their burrows to the surface to feed until the soil becomes saturated (Maelzer 1961).

Litter layers are another environmental feature that have been observed to be related to species distributions. They modify temperature, (Phillips and Cobb, 2005) humidity and prey abundance while providing retreats for invertebrates (Uetz, 1979). The pitfall catch abundances of some species decrease with increasing litter depth, such as the Carabid *Nebria brevicollis* (Greenslade, 1964) and Lycosidae spiders (Uetz, 1979), while others increase in abundance, such as Gnaphosidae, Clubionidae and Thomisidae spiders (Uetz, 1979). The structure of litter has an effect, where its density may deter carabids but favour slender staphylinid beetles (Thiele, 1977). Coarse woody debris (CWD) which consists of dead wood such as fallen trees and branches, broken wood and, sometimes, stumps and standing dead trees (Woldendorp *et al*. 2005) provides habitat for invertebrates and fungi during varying stages of its decay (Grove and Bashford, 2003; Yee *et al*. 2001). It decomposes more slowly in drier, cooler forests. (Woldendorp *et al*. 2005).

Edges of habitats introduce another variable that affects distribution of species. Edges provide a transition between two habitat types and result in an overlap of species, including those preferring edges *per se* (Aspey 1976). Thus habitat edges contain more beetle species (Hobbs *et al*. 2003) and spiders (Luczak 1979) than interiors. Baker *et al*. (2007) found that the edge effect extended 22 m into a forest before the beetle assemblage was 95% similar to interior wet eucalypt forest. In wet forests edge effects on temperature and humidity are detectable within 10 m of an edge while light intensity effects have been found to penetrate 50 m in wet forests (Westphalen 2003) and 100m in *Eucalyptus regnans* forest in Victoria (Dingan and Bren 2003). Dingan and Bren (2003) found that light dropped rapidly in the first 10-30m and penetrated further higher in the canopy.

Numerous beetles are known to have lifecycles associated with fungi and slime moulds, such as Leiodidae species associated with luminous *Pleurotus* species, bracket fungi, *Amanita* and *Tremella* species (Newton 1984).

The stage of decay and lifespan of fruiting bodies of fungi influence their colonisation by invertebrates. Early colonisers of fungi are attracted by a host's species-specific chemical composition at a stage when the fruiting body is young and highest in nutrients. Early colonisers are usually monophagous on fruiting bodies that have a relatively longer lifespan such as bracket fungi which are suitable for species requiring a longer larval stage. Such monophagous Coleoptera include Ciidae, Anobiidae and Tenebrionidae. Later colonisers of fruiting bodies tend to be polyphagous upon non-specific short-lived fruiting bodies at a later stage of decay when species become more chemically uniform (Jonsell and Nordlander, 2004) and the nutrient quality has decreased (Lambert *et al*. 1980). Polyphagous beetles may be unable to colonise fungi until toxic defense chemicals have disintegrated or evaporated during decay processes (Jonsell and Nordlander, 2004).

Leiodidae beetles are subterranean in fungi and ant nests. Some Leiodidae such as *Eublackburniella* sp. feed on mature spores of slime moulds (myxomycetes)

(Matthews 1982). The mobile, multi-cellular, plasmoidal stage of a slime mould during its life cycle is found within leaf litter or rotting logs (Wheeler 1984). Since germination of slime mould spores is influenced by pH and temperature, it has been speculated by Wheeler (1984) that spores may germinate after passing through the specific pH of a beetle gut.

The *Thalycrodes* genus provides an example of a Tasmanian beetle that lives in bracket fungi on trees. They have mycangia or cuticular pockets which carry fungal spores that inoculate trees so that fungi is available for their developing larvae (Crowson, 1960). Similarly, *Aridius minor* (Latridiidae) has phalanges on its pronotum for transporting fungal spores.

In a similar vein, Cerambycidae have endo-symbiotic yeasts in their gut to help digest cellulose in wood and synthesise chemicals such as steroids. Yeasts are transferred to the next generation from pouches near the ovipositor, which contain the yeast, and coat the egg as it is laid. The yeast is then ingested by the larvae when they eat the eggshell (Crowson 1960).

In light of the complexity of fungus-invertebrate relationships, fungi may be significant variables influencing presence of particular beetle species in particular habitats.

Spatial scale has been identified by some researchers as another important variable for species (Anderson *et al*. 2005; Borcard *et al*. 1992; Ferrier *et al*. 1999; Harte *et al*. 2005; Holland *et al*. 2004; Holt and Gaston 2003; Krishnamani *et al*. 2004). It is unlikely that different species respond to their environments at the same scales (Roland and Taylor 1997). Relevant scales are likely to be related to the movement ranges of the organisms (Addicott *et al*. 1987; Cale and Hobbs 1994; Dungan *et al*. 2002; Niemela and Spence 1994; Vos *et al*. 2001; Wiens and Milne 1989; Wiens *et al*. 1995). Unfortunately, little is known about the scales at which a species responds to characteristics of its environment. Flying saproxylic beetles for example disperse at

a scale of 1 square kilometre from source habitat (Okland *et al*. 1996), while Leiodidae (fungus beetles) disperse over smaller distances of 50 m from a source habitat (Rukke and Midtgaard, 1998). Geographic scale may also vary with life history of a species where the food requirements of adults compared with larvae may involve greater dispersal (Holland *et al.,* 2005). The longevity of suitable habitat for different species varies in in forest types. For some species habitat such as fungi or newly dead wood is ephemeral habitat that may be available for a relatively short time while other habitat such as rotting wood may be available for many years (Holland *et al*. 2005).

4.2.1 Pitfall sampling

Sampling methods may introduce an unintended bias on species collected in pitfall containers where the killing solution can attract or repel species. Ethylene glycol can act as an attractant to some species and significantly increase their presence or abundance in pitfall traps (Weeks and McIntyre, 1997), such as ground active carabid beetles, particularly females in early summer (Holopainen, 1990). Propylene glycol provides similar results to ethylene glycol, both of which provide increased captures of invertebrates compared with live traps which are marginally better than water (Weeks and McIntyre, 1997). An alternative alcohol, methylated spirits, attracts some Staphylinidae (Aleocharinae, Omaliinae and *Oxytelus* sp.), Scarabaeidae (*Onthophagus* sp.), *Thalycrodes* sp. (Nitidulidae), Scolytidae and Platypodidae (Greenslade and Greenslade, 1971). Formaldehyde increases capture of carabids and staphylinids but does not seem to affect spiders; while detergent attracts spiders (particularly linyphiids), repels staphylinids and has no effect on carabids (Pekar, 2002). The toxic effects of ethylene glycol, commonly known as antifreeze on other species at a site has been raised by some researchers (Weeks and McIntyre 1997). Ethylene glycol is, however a good preservative for spiders, particularly if traps are left in the field for a month. An alternative, Gault's solution, which is mainly salt water containing a small amount of chloralhydrate, causes spiders to deteriorate (Vink 2002), which makes identification difficult.

Differences in species specific responses to traps themselves has been demonstrated using carabid beetles (Baars 1979; Greenslade 1964) and linyphiid spiders (Topping1993) Other studies reveal that catch ratios of species do not correspond to their abundances in the field (Topping and Sunderland, 1992). Pitfall trap results underestimate the abundance and diversity of foliage spiders. Greenslade and Greenslade (1971), Churchill (1993), Uetz (1975) and Uetz and Uznicker (1976) recommend that interpretation of spider pitfall data should be limited to the wandering spider guild (Lycosidae, Clubionidae, Gnaphosidae, Hahniidae, Ctenidae and some Agelenidae and Pisauridae).

Interpretations of pitfall results can also be ambiguous. For example Joosse and Kapteijn (1968) interpreted a fall in Collembola numbers to post digging-in effects, whereas Jansen and Metz's (1979) model of Brownian motion provides an explanation of their data as 'depletion of victims near the pitfall'.

The effect of trap bias on community assemblages in different habitats (Melbourne, 1999; Mitchell 1963; Phillips and Cobb 2005), such as an increased number of rare species with larger traps (Abensperg-Traun and Steven, 1995), means that pitfall catches may not necessarily present the full picture of the arthropod assemblage in a particular habitat and may skew relative abundances.

Pitfall traps do at least provide a measure of surface activity of species (Chiverton 1984; Churchill 1993; Green 1999; Greenslade and Greenslade, 1971; Uetz 1979; Work *et al*. 2002) which can be dependent on factors such as temperature (Rawthorn and Choi 2001). They enable concurrent sampling across large areas (Spence and Niemela 1994) and have been shown to be effective when estimating relative rather than absolute arthropod richness and activity (Uetz 1976) though even comparative estimates of species abundance across habitats should be interpreted cautiously (Spence and Niemela, 1994).

Pitfall traps are currently the most widely accepted method for conducting ecological

studies on arthropods (Spence and Niemela 1994) because they are labour efficient and inexpensive (Greenslade and Greenslade 1971; Luff 1975; Morrill 1975; Spence and Niemela, 1994; Weeks and McIntyre, 1997), remove diurnal variation in samples due to the time at which hand sampling is conducted (Churchill and Arthur 1999; Gist and Crossley 1973; Green 1999) and enable simultaneous sampling at numerous sites under the same conditions (Brennan *et al*. 1999; Spence and Niemela, 1994; Baars, 1979). Seasonal variation in pitfall trapping is a factor that affects species composition but not species richness, abundance or diversity (Werner and Raffa 2003). The effect of seasonal variation and variation in temperature and microclimate (Adis 1979; Baars 1979; Greenslade 1964; Mitchell 1963; Werner and Raffa 2003) are minimised by pooling the results for species from different seasons. There is an issue that repeated sampling with the same pitfall locations provides samples that are not independent (Borges and Brown, 2001) but this must be weighed against the confounding variation in microclimate and microhabitat that would occur if locations of pitfalls were rerandomised for each sampling season.

Chylnus ater
(Carabidae)

Material and Methods

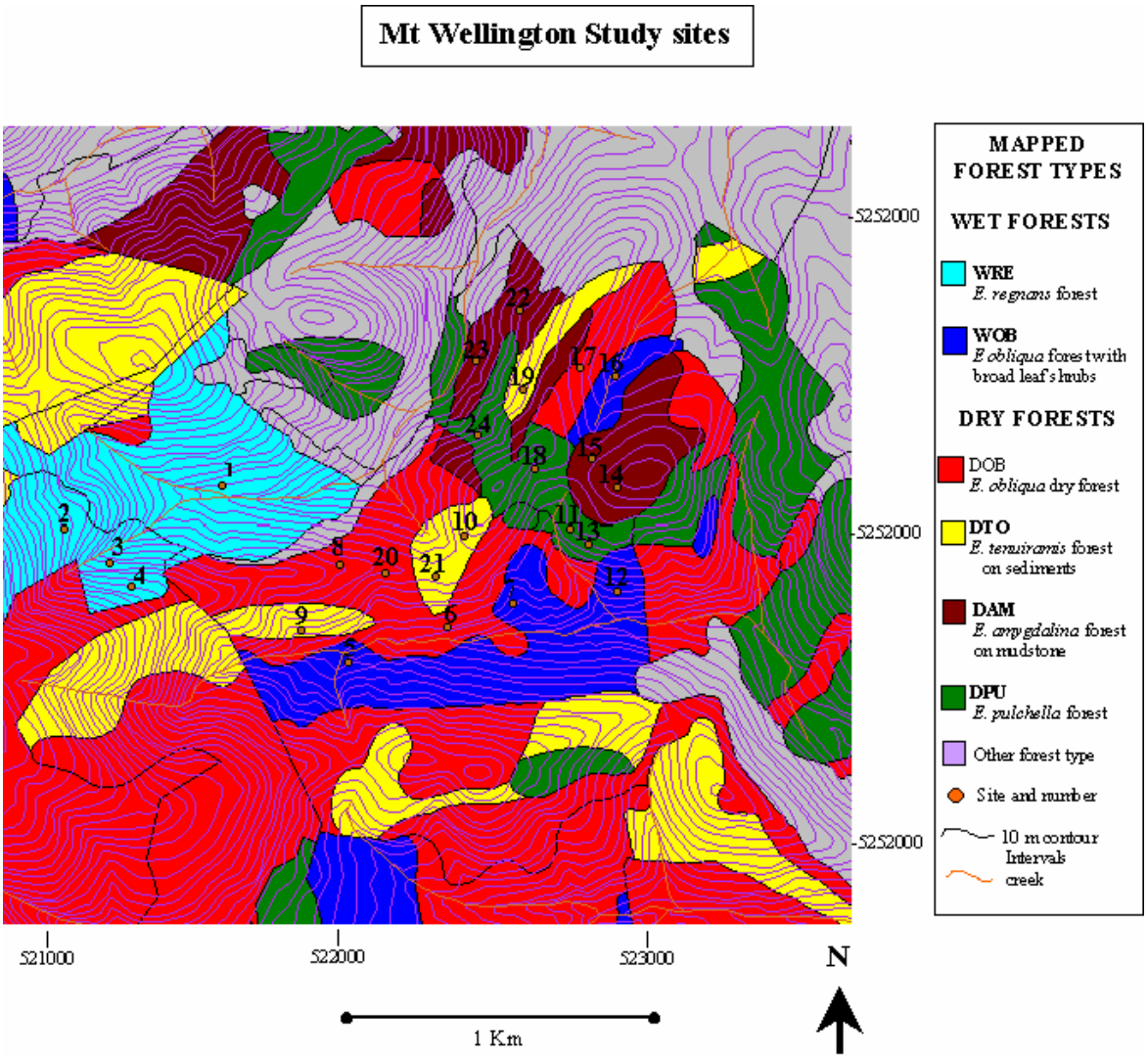
4.1 Study sites

The study was carried out on two scales - intensive and extensive since variation in invertebrate assemblages may be at such a small scale that even sites within ecological vegetation classes differ as much as sites in different ecological vegetation classes (Mac Nally *et al.* 2002). Small scale variation was studied in more detail. A range of environmental variables were measured, including aspects of micro-climate, fungal volumes and soil/litter attributes. These are described in detail later in the chapter.

4.1.1 Location of study sites

The intensive study was carried out in the foothills of Mt Wellington, Hobart. The study area of 1.3 km^2 is bordered by Wellington Park to the West, suburban housing to the North, and a Hobart City Council landfill buffer zone to the Southeast (Figure 2.1). Maps of study sites and distributions of the six eucalypt forest types in this study were created using the open source GIS programme DIVA-GIS v 5.4, available on the web from http://www.diva-gis.org with shapefiles for TASVEG v1.2 2005 available from the Tasmanian Department of Primary Industries and Water.

The extensive study focused upon two of the forest types in the intensive study - *Eucalyptus pulchella* and dry *E. obliqua* in each of 3 regions (Hobart, Levendale and Swansea) (Figure 2.2), totalling 36 sites. The extensive regions, were 50 km apart, spanning 157 km from Pelverata, south of Hobart, to Harding Falls near Swansea on the east coast of Tasmania. The northern sites extended between the coast and the Eastern Tiers, a range of Jurassic dolerite hills with podsolic soils, forested by eucalypts (Harris and Kitchener, 2005) in woodland dominated by *E. amygdalina* and *E. pulchella* with an open understory (Davies, 1988). The sites are all located within the Tasmanian South East (TSE) IBRA bioregion (Figure 0.1). The distribution of the six forest types across Tasmania are shown in Figure 2.3.


Mt Wellington Study sites
5252000
5252000
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N
1 Km
MAPPED FOREST TYPES
WET FORESTS
WRE
E. regnans forest
WOB
E obliqua forest with broad leaf shrubs
DRY FORESTS
DOB
E. obliqua dry forest
DTO
E. tenuiramis forest on sediments
DAM
E. amygdalina forest on mudstone
DPU
E. pulchella forest
Other forest type
Site and number
10 m contour Intervals
creek

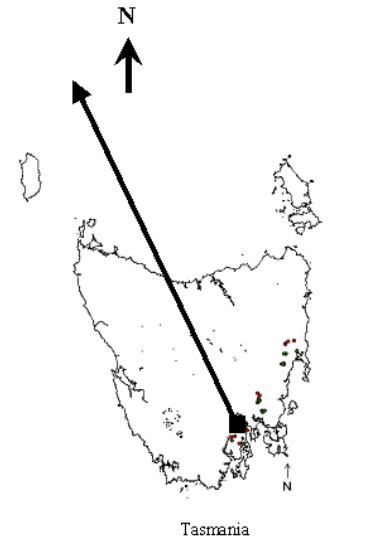

N
N
Tasmania

Figure 2.1 Location of Intensive study sites in the foothills of Mount Wellington

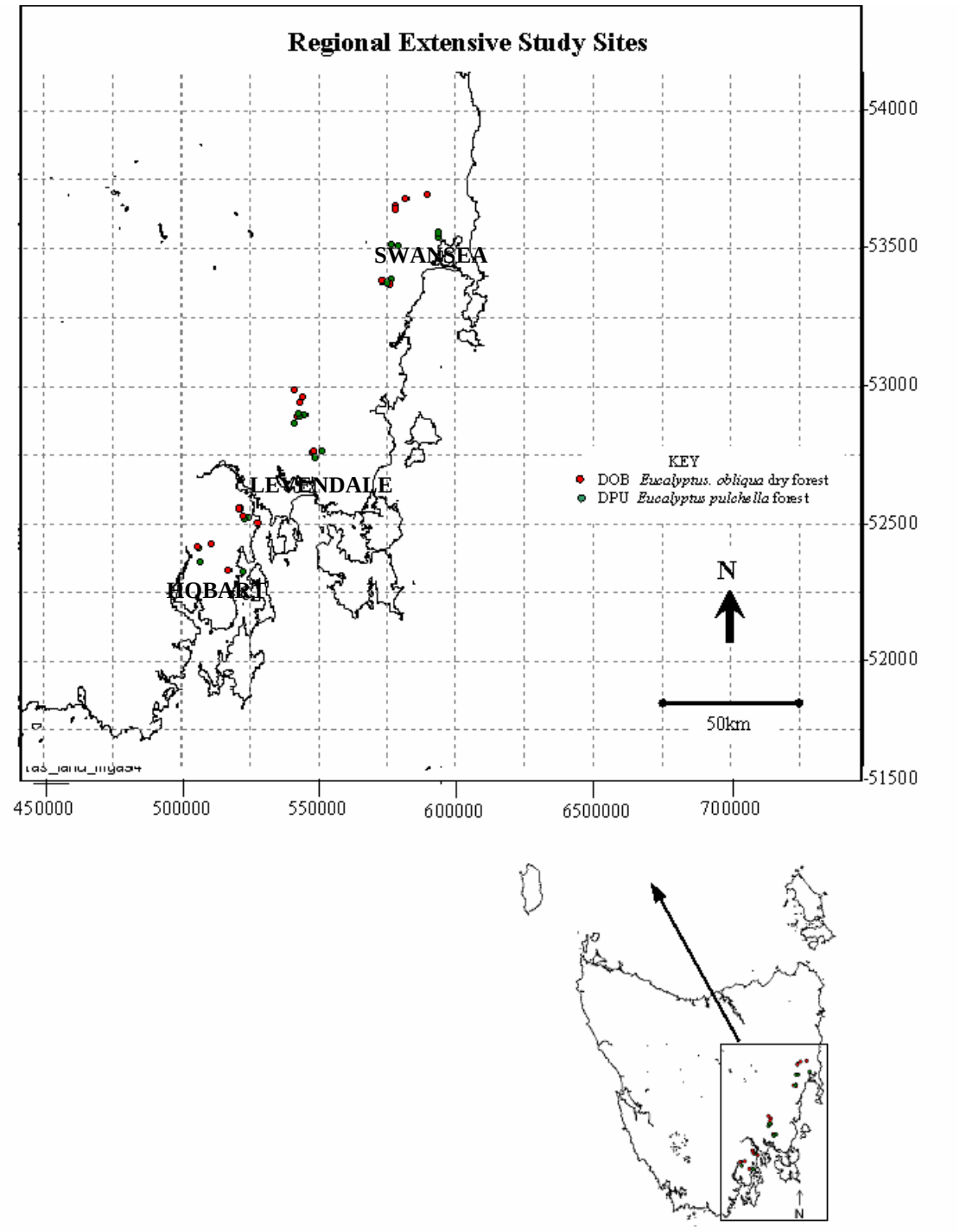
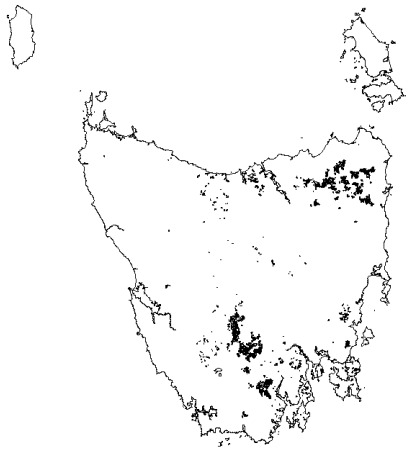
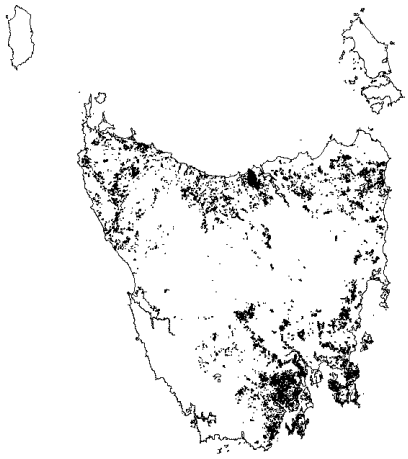


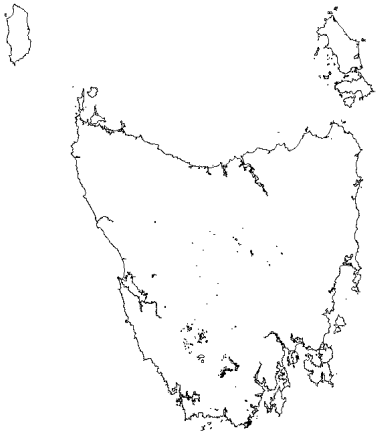
Figure 0.2 Location of Extensive study sites



WRE *Eucalyptus regnans* forest



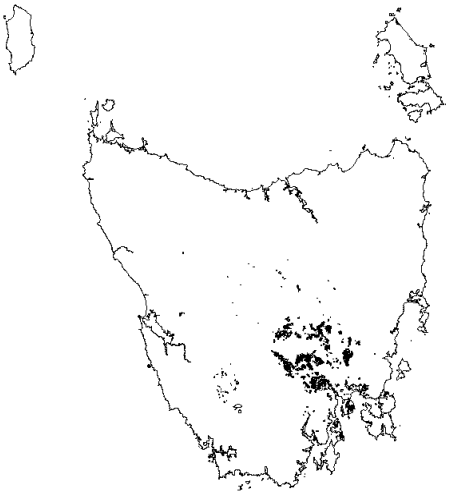
DOB *E. obliqua* dry forest



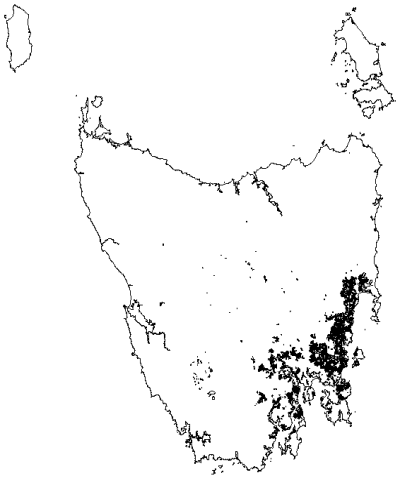
WOB *E. obliqua* forest with broadleaf shrubs

NOT YET MAPPED

DAM E. amygdalina on mudstone



DTO *Eucalyptus tenuiramis* forest on sediments



DPU *Eucalyptus pulchella* forest

Figure 0.3 Distribution of the six forest types sampled by this research (created from shapefiles

for TASVEG v 1.2 2005)

Eastings and Northings for the location of each site are listed in Appendix 1. They were originally recorded under the Australian Geodetic Datum 1966 (AGD66) but have been converted to GDA94 datum. AGD 66 is being replaced with Geocentric Datum of Australia 1994 (GDA94) to make it compatible with global navigation systems such as the satellite-based Global Positioning System (GPS) which uses World Geodetic System 1984 (WGS84) datum. The difference in origin between the two datums is about 200m. If using a pre-2003 map published by TASMAP it will be necessary to convert from GDA94 to AGD66 by subtracting 112m from each of Eastings provided in this study and subtract 183m from each of the Northings. No adjustment is required for a GPS set to GDA94 or WGS84 (http://www.icsm.gov.au/icsm/gda/). Since many of the maps in use are based on the older AGD66 system, both types of data are provided in Appendix 1 for the sites in this study.

4.1.1 Selection of Eucalypt Forest types

TASVEG v1.2 2005 (DPIWE, 2005) provided mapped forest communities from which it was possible to select six adjacent eucalypt forest types. The study area of 1.3km^2 contained four replicates of each forest type, totalling 24 sites. Table 2.1 lists the forest types and the site numbers within each forest type.

FOREST TYPE	RFA (TASVEG 2000 CODE)	TASVEG v1.2 COMMUNITY CODE 2005	SITE NUMBERS Mt Wellington (MW)
Eucalyptus regnans forest	R	WRE	1, 2, 3, 4
Eucalyptus obliqua forest with broadleaf shrubs	OT	WOB	5, 7, 12, 16
Eucalyptus obliqua dry forest	O	DOB	6, 8, 17, 20
Eucalyptus tenuiramis forest on sediments	TI	DTO	9, 10, 19, 21
Eucalyptus pulchella forest	P	DPU	11, 13, 18, 24

Eucalyptus amygdalina forest on mudstone	AI	DAM	14, 15, 22, 23

Table 2.1 Forest types sampled in the study

The proximity of sites to each other minimised variation due to climate, fire events, landscape, geology and soil. Each site was a minimum of 5 m away from tracks to minimise disturbance. It must be noted, however, that presence of certain vegetation types is a result of variation in geology and topography so the location of forest type was not a random variable in the research. For example, the leaves of *E. pulchella* are well adapted to dry conditions and on Mt Wellington it is found on steep, north facing, shallow, dry soils on Jurassic dolerite, particularly ridge tops (Reid and Potts 1999). *E. tenuiramis* occurs on steep north facing slopes of Permian mudstone while *E. amygdalina* occurs on steep north facing slopes of Triassic sandstone. All three of these eucalypt species are replaced by *E. obliqua* on cooler and wetter south facing slopes, regardless of the underlying rock type (Reid and Potts 1999; Williams 1991). *E. globulus* and *E. regnans* are found on deeper, moist, well drained soils.

Four of the monocalypts selected in this study were singularly dominant in their forest type: *E. obliqua*, *E. regnans*, *E. amygdalina* and *E. tenuiramis*. As is typical for *Symphomyrtus* species (Reid and Potts 1999), *E. globulus* and *E. viminalis* were co-dominant with a monocalypt, *E. pulchella*. Co-occurrence of a monocalypt with a symphyomyrt is typical of forests linking dry sclerophyll to moist forests where Ashes such as *E. obliqua* and *E. regnans* dominate (Duncan 1999). Harris and Kitchener (2005) provide descriptions of the mapped Tasveg v1.2 forest types that are listed in Table 2.1. Photos of the sites, displaying variation in understory cover, appear in Figure 2.4.

WRE *Eucalyptus regnans* forest, site 3

WOB *Eucalyptus obliqua* forest with broad leaf shrubs, site 16

DOB *Eucalyptus obliqua* dry forest, site 17

DTO *Eucalyptus tenuiramis* forest on sediments, site 19

DPU *Eucalyptus pulchella* forest, site 13

DAM *Eucalyptus amygdalina* forest on mudstone, site 15

Figure 2.4 Site photos representing the variation between forest types.

4.1 Sampling of spiders and beetles

4.2.1 Experimental design

A stratified random pitfall sampling regime based on forest type was employed for the Mt Wellington sites. Four sites within each of six adjacent TASVEG Vegetation types were surveyed for beetle and spider species using 10 pitfall traps at each site during three seasons.

Pitfall traps were used in this study to assess relative abundance of beetles and spiders in different eucalypt vegetation types. Small diameter (4.2 cm) plastic traps were selected to reduce impact on larger non-target species such as frogs and lizards. Traps were located within a 200 m^2 area at each site. Ten pitfall traps were placed at 10m intervals along two 40 m rows that followed a contour. Each row was 5 m apart.

Each pitfall trap was buried to ground level so that the top was flush with the soil and half filled with Gault's solution containing a small quantity of chloralhydrate as follows: sodium chloride 50g/l, potassium nitrate 10g/l, chloralhydrate 10g/l, and glycerine 20ml/l.

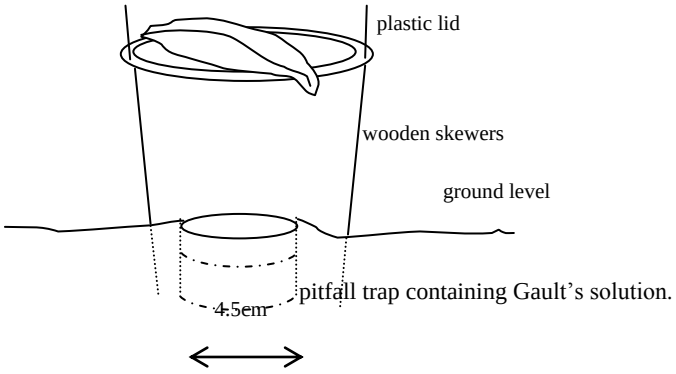


Figure 0.5 Pitfall trap design used in sampling

Gault's solution was selected by Meeson (2006) when establishing the sites for

research on ants but it was later found to be a poor preservative for spiders (Vink 2002).

A 10 cm plastic lid was secured as a roof over the trap with two wooden skewers pushed into the ground. The lid was tilted for rain run-off (Spence and Niemela 1994) and was covered with small pieces of bark and leaves to camouflage it from ravens and other birds as well as to reduce evaporation of liquid in the traps (Figure 2.5). Lid transparency has been shown to have no microclimatic effect that biases pitfall catches towards, for example, carabid beetles (Phillips and Cobb 2005).

Each trap remained open in the field for twenty-five days. For the intensive study in the Mt Wellington foothills, sampling was conducted in spring (November 2002), summer (February 2003) and autumn (April 2003). Sampling for the extensive study was conducted in spring (November 2003).

Once ants had been removed by Meeson (2006), pitfall catches from all 10 pitfall traps at a site were pooled into one container for sorting and identification of beetles and spiders, although this resulted in loss of information for later analysis.

4.2.1 Identification of species and morphospecies

Spider and beetle specimens collected in the pitfall traps were identified to morphospecies and later identified to species level where possible with assistance from Dr Peter McQuillan (Coleoptera) and Bec Harris and Lisa Boutin (Araneae). Access to the Department of Primary Industries and Forestry Tasmania insect collections enabled further identification of Coleoptera, while Liz Turner provided access to the Tasmanian Museum and Art Gallery spider collection.

An extensive file of original descriptions of species was compiled and for large families with many unnamed species, matrices of characteristics that distinguished species were developed. A reference list of taxonomic literature used for identification appears in Appendix 7. Species were photographed and a voucher collection was deposited at the University of Tasmania in the Biogeography Fauna Laboratory of the School of Geography and Environmental Studies.

Biophysical attributes

4.2.1 Aspect/Altitude/Slope

Altitude, aspect and slope were recorded as continuous variables. Altitude was determined in metres from the 1:20,000 series of maps. Aspect to the nearest 10 degrees was measured with a compass and slope was measured in degrees using a clinometer.

A table of the site characteristics are presented in Appendix 1.

4.2.1 Soil

The focus of this study is on litter invertebrates, but owing to overlap of species in soil and litter microhabitats (Coy *et al*. 1993) it was necessary to include soil variables as possible factors that may influence invertebrate assemblages collected from litter.

4.2.4.1 Soil Hardness

Soil hardness was measured as resistance to penetration. It varies with soil type and increases with higher bulk densities, while it decreases with increasing water content and increases with decreasing particle size due to lower matric potential which is a measure of the strength with which the soil holds water (Bengough *et al*. 2001).

An *Ele* pocket penetrometer with a cylindrical tip of 0.6 mm was used in the field to measure soil strength (resistance to penetration) as unconfined compressive strength of the sample in kgf/cm^2 on a scale from zero to five. (Shear strength equals this reading divided by 2). A wider tip of 26 mm inserted to the same depth of 0.6 mm was used to increase accuracy for softer soils where readings were close to zero.

When the penetrometer encountered a stone the result was discarded and the measurement was repeated nearby to reduce outlier data that would bias comparisons across sites (Bengough *et al*. 2001).

A minimum of seven independent replicate measurements were required based on formula (1) (Bengough *et al.* 2001) for a 95% confidence interval (ASAE, 1969).

$$N=\left[\frac{2CV}{L}\right]^2 \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (1)$$

Where N = number of required measurements (N) taken at least 1 metre apart; L = the 95% confidence interval as a percentage of the mean and CV = the coefficient of variation.

In total, fifteen replicate penetrometer readings at randomly located distances greater than 2 m apart were recorded for each site in winter and the following summer. Soil hardness was recorded as a continuous variable.

4.2.4.2 Chemical analysis of soil

To collect samples, the litter layers (undecomposed O1 horizon and decomposing O2 horizons) were swept aside and a soil core of 5 cm diameter x 10 cm deep was taken using an aluminium tube which was twisted by hand into the soil. The depth of the topsoil (A horizon) and subsoil (B horizon) in the core was recorded. The topsoil and subsoil were placed in separate containers. Additional cores of each horizon were taken from adjacent soil until a 500 cm^3 container was filled to provide enough material for measuring moisture content and chemical analysis. Six independent, random replicates of each horizon were collected at each site at distances greater than five metres apart. Containers were immediately sealed and kept cool (Rayment and Higginson 1992) to prevent water loss and minimise chemical changes prior to analysis.

Samples for chemical analysis were collected in summer and air dried in a laminar flow cabinet so that samples would remain cool and could dry as quickly as possible to reduce chemical change.

Air dried soil was sieved to remove gravel and particles > 2 mm. Sieved samples were

ground with a mortar and pestle and sieved through 0.5 mm mesh ready for chemical analysis.

The nitrogen, phosphorus and organic carbon content of the soil was determined using methods described by Rayment and Higginson (1992). For example, available Phosphorus was measured by the Bray extractable phosphorus method which extracts phosphorus compounds soluble in acid. The carbon to nitrogen (C:N) ratio was calculated from the values of available carbon and nitrogen. Available rather than total chemical content was a more relevant measure of soil chemicals since it is a measure of the amount of a chemical available to biotic components such as plants and microbes on the forest floor (Vesterdal 1998).

4.2.1 Soil pH

Tests for soil pH were carried out in the field to prevent error due to alteration of pH during transport from biological activity, temperature increase and chemical change (Brower *et al*. 1989). A kit by Inoculo Laboratories, Victoria, was used where a small soil sample was mixed with indicator solution, then dusted with white barium sulphate powder. This allowed the colour of the pH solution to become visible and be matched against a colour chart to determine the pH within an accuracy of half a pH unit. Five random samples were measured for soil pH at each site and the results averaged for each site.

4.2.1 Microclimate

4.2.6.1 Canopy Cover

To measure canopy cover, a *Canon* digital camera with a 38 mm lens and F-stop 4.5 was placed on the ground next to each pitfall trap to obtain an image of the canopy directly above (Figure 2.6). From each photo the percentage of canopy cover was calculated by converting

each photo to grey scale, pixellating each photo and assessing each pixel as either black (canopy) or white (no canopy). The advantage of this method was that it provided a measure of penetration of solar radiation adjusted by canopy and sub canopy density. A categorically scored canopy cover index would have under-estimated solar penetration by ignoring the effect of the pendulous nature of eucalypt leaves (Baehr 1990).

Figure 2.6 Sample photo of the canopy taken from ground level for site 4, from which average percentage of canopy cover was calculated.

4.2.6.2 Solar Radiation

Solar radiation and adjusted solar radiation were determined for summer and winter.

Solar radiation was determined using Nunez's estimation of solar radiation received on slopes in Tasmania (Nunez 1983, p. 156-157) from equation (2).

Incoming solar radiation ($K_C\downarrow$) = direct radiation on surface + diffuse radiation from the sky incident on the surface + diffuse radiation from reflection of global radiation by the ground.

$$K_C\downarrow = I_o\ \tau \cos\gamma + D\ .VF + G_c\ \alpha\ (1\text{-}VF) \quad \ldots\ldots\ldots\ldots\ldots\ldots(2)$$

where: I_o = solar constant = 1353 Wm^{-2}

τ = the transmission of the atmosphere to direct radiation

γ = the angle of incidence of direct radiation with the inclined surface

($\cos\gamma = \sin Z.\cos\phi.\sin X.\cos Y + \sin Z.\sin\phi.\sin X.\sin Y + \cos Z.\cos X$

where Z, ϕ = zenith and azimuth angles for direct solar radiation;

X,Y = zenith and azimuth angles for the normal to the surface)

D = diffuse radiation incident on a horizontal surface = 0.6Wm^{-2}

VF = the sky view factor (from 0.5 for a vertical surface to 1 for horizontal)

α = albedo of the surface (a mean of 0.2 between eucalypt forests and dry grasslands was used)

G_c = global solar radiation on a horizontal surface = $I_o \tau \cos Z + D$ (Z= solar zenith angle)

Estimations of summer solar radiation for southern Tasmania range from a maximum of 22.0 MJm^{-2} per day on a horizontal surface in December to 9.0 MJm^{-2} per day on a vertical south facing slope. In winter solar radiation reaches a maximum of 9.0 MJm^{-2} per day on a north facing slope of 65^o and falls to 1.9 MJm^{-2} per day on a vertical south facing slope (Nunez 1983).

Aspect and slope data for each study site enabled an estimation of solar radiation to be read from Nunez's (1983) charts.

Nunez's model applies to bare ground. An innovation of this study was to adjust the solar radiation figure to provide a value for the amount of radiation falling on litter under a canopy. This entailed multiplying solar radiation (Nunez, 1983) by the percentage of non-canopy cover.

Adjusted solar radiation represented the solar radiation incident on the litter layer beneath the canopy.

Adjusted solar radiation = solar radiation x (100 - % canopy cover measured from the litter layer)/100

……(3)

4.2.6.3 Sub-soil and Ground Surface Temperatures

Soil temperature may be considered to be an index of canopy cover, litter depth and soil moisture and thus it is expected that a correlation will exist between this data. To measure suface litter or bare ground temperature, a *Raytec* Lasar Temperature Gun was directed at a randomly selected spot on the ground and scanned over an area of

half a square metre for three seconds. The temperature gun was set to display the average temperature during that time and this was recorded. This was repeated until 5 readings for litter covered surfaces and 5 readings for bare ground were obtained. Each set of 5 readings was averaged to provide an average surface temperature for litter cover and bare ground at each site. Not all sites had both litter cover and bare ground so only relevant recordings were made. Measurements were made for each site during summer and winter. Results are recorded in Appendix 6.

Sub-soil temperatures were taken at 5 cm below the surface by digging down 5 cm with a spoon and immediately directing a *Raytec* temperature gun at the lowest point of soil. Ten measurements were recorded and averaged for each site. Measurements were conducted during summer and winter.

4.2.6.4 Surface Air Humidity

A *TempTec* instrument was used to measure air humidity at ground level. Five readings at each site were averaged to provide an average measure of humidity for each site. All readings were done during the morning on the same day to minimise variations in weather conditions between sites and provide a rough measure for comparison across sites.

4.2.6.5 Soil Moisture

Since soil moisture varies according to rainfall, drainage, waterholding capacity of the soil and evapotranspiration (Brower *et al.* 1989) a full profile of soil moisture requires multiple sampling across seasons. This study was only able to provide a single snapshot to compare relative soil moisture across sites. Six separate randomly selected, replicate samples were collected at each site for individual analysis. This

was preferable to the common practice of pooling six soil samples and then subsampling six times from the pooled samples for each site (Hanna 1964) since it would provide information on the variation of soil moisture within a site. Soil moisture was measured from the soil samples collected for chemical analysis (section 2.2.4.2).

To calculate the percent water content of soil, a thermogravimetric method for soil water content was used. Water held by surface tension was evaporated from a weighed soil sample, with gravel and rocks > 2 mm removed (Rayment and Higginson 1992), in an oven at 105 ^{o}C for about 24 hours until no further change in mass occurred (Gardner *et al*. 2001; Brower 1989), i.e. where, under procedures of the International Standards Organisation, during a further 4 hours of drying the mass difference was not greater than 0.1% (ISO 1993). Rather than cool soil in a desiccator before weighing, each sample was weighed while hot from the oven to reduce moisture uptake. The loss of weight represents moisture content and is expressed per 100g of dry soil:

Soil moisture = (wet weight - dry weight) x 100% / dry weight

……..(4)

It must be noted that not all water is removed at 105 ^{o}C. Adsorbed and structural water are not removed until 110-160 ^{o}C and 400-800 ^{o}C respectively so they are traditionally not included in measures of soil moisture. Some error may also be introduced for organic soils that may lose other components apart from water at 105 ^{o}C (Gardner *et al*. 2001).

4.2.1 Ground Cover

Four intercept transects were conducted at each site The method was to proceed a randomly selected number of paces along the site from the first pitfall trap and carry

out a 20 m intercept transect in a randomly selected direction 10m forward and 10 m backwards from that point. Ground cover was recorded at 10 cm intervals and classified as litter, bare ground, rock, coarse woody debris, grass, shrubs, herb, tree (eucalypt), tree (understorey), fern, tree (sapling), understorey tree (sapling), mossy rock, mossy coarse woody debris, mossy tree (eucalypt), mossy tree (understorey). Results of the transects were averaged for each site.

4.2.1 Litter Depth

Litter depth data was obtained from five transects at each site by proceeding a randomly selected number of paces along the site from the first pitfall trap and marking out a transect in a randomly selected direction 10 m forward and 10 m backwards from that point. Five measures of litter depth were obtained for each transect by taking a measurement at 4 m intervals. Where intercept transects were being conducted litter depths were measured concurrently along the same transects.

4.2.1 Rotten wood volume

Fixed-area plot sampling was undertaken in randomly located plots of 250 m^2 (50 m x 5 m) in which the volume of all rotting logs was calculated.

4.2.1 Basal Area

The Basal Area of trees at each site was estimated using the Bitterlich method named after the Austrian forester who developed it in the 1930s (Brack and Wood 1997) with point sampling. A Bitterlich Wedge, consisting of a wooden crosspiece gauge was held at arm's length over a randomly chosen spot within the site and rotated horizontally 360 degrees over the spot while the number of trees with breast height equal to, or greater than the width of the crosspiece from that distance, were counted and recorded as m^2/ha. Using a rod of length 50 cm with a crosspiece of 1 cm provided a 50:1 ratio so that the direct count of trees was equal to the basal area in m^2/ha. The stick was held parallel to the ground to compensate for slope effect which

would cause an underestimation of number of trees.

This procedure was conducted five times from random locations at each site. The resulting 5 scores were averaged to provide the mean basal area of trees in square metres per hectare for that site.

4.2.1 Plant Communities

Major vascular plant species identified during a 20-minute survey of each site were recorded and abundance assessed using the Braun-Blanquet score where a score from 1 to 5 was assigned to each species in that vegetation type according to its percentage of coverage of the site.

Braun-Blanquet score	Species cover %
1	< 1%
2	1-5%
3	6-25%
4	26-50%
5	51-75%
6	76-100%

Table 2.2 Braun-Blanquet score for vegetation cover

4.2.1 Fungi

A snapshot sample of fungi species was provided by recording the species and volume of macro fungi above the ground at each site during autumn (May). The volume of each fruiting body was calculated from measurements taken of the diameter and depth of the pileus (cap) and diameter and length of the stipe, where relevant. Photographs were taken to aid identification from reference books (Fuhrer, 2001; McCann, 2003) and from the expertise of Sapphire McMullan-Fisher.

4.1 Statistical analysis

4.3.1 Diversity in species assemblages among sites

Diversity is an index of the variety (species richness) and relative abundance (evenness) of species in a sample (Magurran 1988).

Species turnover, which refers to change in species diversity along an environmental gradient (Vellend 2001) was not calculated as the sites were not ordered *a priori*, but a more general measure of beta diversity was calculated from the large number available to measure of the change in species among sampled sites.

Local variation in beta diversity among adjacent forest types was investigated by comparing species richness using a modification of Whittaker's beta biodiversity index (Harrison *et al*. 1992). The modification allows for uneven numbers of samples by dividing Whittaker's Index by the number of sites minus one and expressing the result as a percentage.

$$\beta_1 = 100 \text{ x } [(S / \alpha) - 1] \ / (N - 1) \qquad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots.(4)$$

N = number of sites
α = the maximum number of species recorded at a site
S=the total number of species in the study

The index ranges from 0 (completely similar) to 100 (completely dissimilar).

Fundamental to the choice of appropriate statistical tests was the undertaking of exploratory data analysis. Scatterplots of combinations of pairs of variables were used to identify correlations that may interfere with some analyses, as well as to check the normality of the data, homogeneity of variance and sample distribution so that outliers

that may require log transformation of the data could be identified.

4.3.1 Looking for patterns in species assemblages among sites

A preliminary NMDS ordination of dissimilarity of species distribution across sites was conducted to see which sites clustered together in species space due to shared species and whether these clusters corresponded to forest type. If identifiable groupings could be discerned, then more rigorous tests could be conducted to determine whether any of the measured environmental variables contributed towards the assemblage patterns.

4.3.1 Do assemblage patterns correspond to forest types?

More rigorous investigation of the relationship between patterns in beetle and spider distributions and forest type was provided by non-parametric multivariate analysis of variance and analysis of similarity to test the null hypothesis that the means of the assemblages grouped by forest type are not different in their multivariate means or in their dispersion. The purpose was to determine whether species from the same forest type are more similar than those from different forest types. In addition, *a posteriori* pairwise tests were conducted to compare which forest types had significantly different assemblages to other forest types. The NPMANOVA (Anderson, 2003) programme was used for beetles and spiders in the local scale Mt Wellington study, which was a one-way simple ANOVA design. PERMANOVA (Anderson, 2005) was appropriate for the two way crossed factor design of the more extensive regional study. NPMANOVA and PERMANOVA have been applied to analyses of beetles in wildlife habitat strips (Grove and Yaxley 2005), edge effects on beetle (Baker *et al.* 2007; fauna inhabiting kelp holdfasts (Anderson *et al.* 2005) and a re-analysis of intertidal gastropods (McArdle and Anderson 2001).

PERMANOVA and NPMANOVA provide a semi-parametric multivariate analysis of

variance that simultaneously compares group centroids for a linear model. The programmes were developed to overcome the limitations of ANOSIM and are freely available from http://www.stat.auckland.ac.nz/~mja/Programs.htm. By calculating variance as the Sums of Squares (SS) of distances from observations to centroids, a variety of distance measures can be used apart from Euclidean, thereby avoiding the limitations of a multivariate ANOVA (MANOVA) analysis of several dependent variables where there are many zeroes in the data (Field et al. 1982; Legendre and Legendre 1998).

NP-MANOVA analysis of the Mt Wellington data was conducted for a one-way design to compare species recorded in each of the different forest types with sites grouped by forest type (6 factors) and 4 replicates of each. PERMANOVA analysis of the more extensive regional sites was conducted for a two way crossed model for fixed factors 'region'(3 levels) and 'forest type' (2 levels) with 6 replicate sites for each. For both analyses data were fourth root transformed, a severe transformation to overcome the large differences in abundances from hundreds for some species to zeroes for many others. Distances between pairs of samples were calculated using the Bray Curtis dissimilarity measure which is appropriate for data with many zeroes because it does not count joint absences as similar (Clarke *et al.* 2005; Clarke and Ainsworth 1993; Field *et al.* 1982).

From the dissimilarity matrix the sum of squared distances among groups in the half matrix, divided by the number of samples yielded the total sum of squares (SS_T):

$$SS_T = \frac{1}{N}\sum_{i=1}^{N-1}\sum_{j=i+1}^{N} d_{ij}^2 \qquad \text{.....(5)}$$

Similarly, the sum of squared distances within groups (SS_W) was calculated by dividing the sum of squared distances between replicates in the same group by the number of replicates in that group:

$$SS_W = \frac{1}{n}\sum_{i=1}^{N-1}\sum_{j=i+1}^{N} d_{ij}^2 \varepsilon_{ij} \qquad \text{.....(6)}$$

for $\varepsilon_{ij} = 0$ if observations *i* and *j* are in the same group and 1 if they are in different groups (Anderson, 2001). The among group sum of squares could then be calculated as

$$SS_A = SS_T - SS_W \qquad \text{……..(7)}$$

A pseudo *F*-ratio test statistic for the factor 'forest type' was calculated as a ratio of the sum of squared distances among groups and the sum of squared distances within groups:

$$F = \frac{SS_A / (a-1)}{SS_W / (N-a)} \qquad \text{…….(8)}$$

where a = number of groups, n= number of replicates, N = number of samples = a x n

The test statistic was a pseudo F-ratio because a non-Euclidean distance measure (Bray-Curtis) was more appropriate for the data and the variables may not be normally distributed, making standard F tables inappropriate (Anderson 2005). Under these circumstances a permutation procedure was used to randomly reallocate samples to any forest type to test a null hypothesis for no effect of forest type by calculating an F_{random}-ratio for all possible random combinations of samples (shuffling of rows) in the original data matrix. The F_{random} value of the permutations was compared with the experimentally derived *F-ratio* to determine a *P* value (Anderson, 2005):

$$P = \frac{\text{Number of } F_{random} \geq F}{\text{Total number of } F_{random}} \qquad \text{…….(9)}$$

The distribution of the F ratio under the null hypothesis of no difference between the treatment groups was compared to the observed F-ratio. The F_{random} value was derived from 9999 unrestricted permutations of raw data. If any of the main effects were significant, *a posteriori* pairwise comparisons of variables were requested and the significance of the pairwise tests for differences between assemblages in different forest types were corrected for multiple comparisons using sequentially adjusted Bonferroni probabilities.

A non-metric MDS plot of 4^{th} root transformed abundance data with Bray-Curtis distances was created in 'R' to provide a visual indication of variation in the data.

PERMANOVA and NP-MANOVA can indicate that a difference between groups is significant if there is a variation in spread among groups with some groups widely dispersed and others clumped (Anderson 2003, 2005). Therefore, if a significant result was obtained from PERMANOVA or NP-MANOVA analyses, investigation was undertaken to determine whether the significant difference between groups was due to dispersion differences among groups or to location (Anderson, 2004). To do this, a programme called permutational analysis of multivariate dispersions (PERMDISP) (Anderson, 2004) was used to test the homogeneity of the data by comparing the multivariate dispersion among groups of the Bray-Curtis dissimilarity measure. The PERMDISP programme calculates distances of observations from their centroids and then uses an ANOVA procedure to compare the average of the distances among groups (Anderson, 2004). Through the programme's use of distances of observations from centroids, a variety of distance measures can be used apart from Euclidean distance.

While it is preferable to use Euclidean distance as a distance measure to preserve the centroid as the arithmetic mean of the original observation and the variable in PERMDISP analysis, the Bray-Curtis distance measure was selected to retain consistency with the distance measure used in the NP-MANOVA analyses. This enabled a comparison to be made with the original analysis. Similarly, transformation of abundance data to fourth root was selected for consistency with the NP-MANOVA tests even though transformation affects the heterogeneity of the data which in turn affects dispersal of points which is what was being examined. A total of 9999 permutations of the raw data were used.

PERMDISP made it possible to tease out whether significant results for differences in

species assemblages in different forest types in PERMANOVA were due to location and/or relative dispersal of the data.

In a similar vein to nonparametric multivariate analysis of variance, an analysis of similarity (ANOSIM, Clarke 1993) was conducted to test whether the grouping of beetle assemblages by forest type resulted in more similarity within forest types compared with between forest types. The procedure has been used to analyse associations between matrices of species (Gibb and Hochuli 2002; Major *et al*. 1999; Murray *et al*. 2006; Somerfield *et al*. 2002).

The null hypothesis tested was that the distances between pairs of samples between groups were the same as the distances between pairs of samples within groups. The technique used a non-parametric permutation technique on a Bray-Curtis dissimilarity matrix transformed into a matrix of rank similarities where the elements were ranked so that the highest similarity has the lowest rank of one. The aim was to test for differences in species assemblages in the *a priori* grouping of forest type.

An R statistic was calculated for the observed data:

$$R = \frac{(\bar{r}_b - \bar{r}_w)}{(M / 2)} \qquad \text{.....(10)}$$

where $\bar{r}_b$ is the average of all pairwise rank similarities between site
$\bar{r}_w$ is the average of all pairwise rank similarities among replicates within sites
for $M = n(n-1)/2$ where n is the number of samples

A second R statistic was calculated for each permutation of labels randomly reallocated to a different sample and the distribution of this R statistic under the null hypothesis of no difference between forest type was compared to R for the real data.

(4 replicates of 6 treatment groups gave 4.5E+12 permutations so 10,000 permutations were conducted).

The null hypothesis was rejected at a significance level of 100 x (t+1)/(T+1) % where t is the number of simulated R ≥ observed R and T is the total number of simulations.

ANOSIM is sensitive to zero inflated data, so species whose abundance was less than 5 were excluded. This is unlikely to affect the results since species with low distributions are unlikely to be present at enough sites to affect the results. The resulting boxplots portrayed the dispersal of the data.

4.3.1 Detecting environmental variables in assemblage patterns

Rank dissimilarity between sites was mapped to determine whether there might be any groupings of sites by similar variables and whether these groupings corresponded to forest type.

An exploratory NMDS of species distributions was overlaid with environmental variables represented by different sized circles to visually compare whether their variation corresponded to species distributions. Forest type was excluded from the variables in order to detect patterns arising from other variables.

Canonical Analysis of Principal Coordinates (CAP) (Anderson, 2004) was conducted to provide a measure of the contribution of each environmental variable to the variation in the species data, thereby examining how assemblages vary across environmental gradients (Baker *et al.* 2007; ter Braak 1986). This enabled the variables with the greatest influence on the data to be identified and provided a basis for selection of a smaller number of variables for further analyses using the permutational selection procedure, BIOENV. CAP was employed in preference to Principal Components Analysis (PCA) which assumes multivariate linearity of the data (Anderson and Willis 2003; Kempton 1977; Legendre and Anderson 1999; Palmer 1993; ter Braak 1986).

CAP provided a canonical analysis of the effect of the matrix of environmental variables (standardised) on the species variables (transformed to ln+1). A reduced set of environmental variables was used to constrain the ordination since use of all environmental variables would have provided an unconstrained analysis similar to an NMDS. Bray-Curtis dissimilarities were centred to generate a Gower's centered matrix from which an eigenanalysis provided eigenvalues which were the squared canonical correlations of the matrix from which the test statistic, the greatest root statistic, δ^2, was calculated. The p value for the statistic was the result of permutations of groups, with 9999 permutations selected. Visual support for the results was provided by plotting the eigenvectors from the principal coordinates analysis (PCO axes), as an unconstrained MDS (Anderson, 2004).

4.3.1 Detecting which environmental variables are important

If a difference between assemblages in different forest types was established exploratory analysis of environmental variables was undertaken to identify which environmental variables might be important to the distributions of invertebrates (De'ath 2002; Moore *et al.* 1991; Woehler *et al.* 2003). Regression tree models were built in R (version 2.4.1) using the tree package (Ripley, 2007) to determine which of the numerous environmental variables measured were important to beetle and spider distribution. Regression trees were appropriate because the species data are continuous, although analyses assume that data are normally distributed. Histograms of species data (abundance vs frequency) was used to verify this normality. (Moore 1991)

Regression trees employ a nonparametric, iterative method that partitions multivariate data dichotomously into ranked subsets based on the differences among *a priori* groups. Partitions are selected by the programme where they minimise deviance in the data. In the output trees, the improvement in prediction error obtained by the split is

proportional to the depth of the tree below each split. At each node the variable that distinguishes best between observations is identified along with the value at which the split occurs. The leaves of the tree display the mean number of species present in that particular split of the data.

Before building regression trees, rarer species (less than 5 individuals present in the whole dataset) were removed from the species matrix since their occurrence was not significant enough to detect patterns with environmental variables. All environmental variables were used.

PCA was used to identify variables that described most of the differences in environmental variables between sites. The function BIOENV (Clarke and Ainsworth 1993) was applied to the question of which environmental variables had a significant role in explaining the variability of species distributions rather than site variation. BIOENV was appropriate for comparing two matrices of variables (biological and environmental) to explore which variables were significant. It has been more commonly applied to marine and freshwater analyses of assemblages (Clarke 1993; Frost *et al.* 1999; Whitman *et al*. 2004).

BIOENV sought the best subsets of environmental variables by estimating the correlation between ranked Bray-Curtis dissimilarity among species and ranked Euclidean dissimilarity among standardised environmental variables for the sites. It sequentially added variables to the predicted model that would provide the highest Spearman rank correlation between elements of the two dissimilarity matrices (Clarke and Ainsworth 1993). The BIOENV procedure in the Vegan package (version 1.8-5, Oksanen *et al*. 2007) for 'R' takes some time for large numbers of variables, in this case $2^{56} - 1 = 7.2 \times 10^{16}$ permutations. Therefore variables were first reduced, based on information from other analyses and removal of redundant correlated variables. BIOENV enabled a further reduction of the number of most important environmental

variables which was required before further investigation of variation could be explored.

If there was an indication that vegetation type was a significant variable for distributions of species, a hierarchical partitioning (Chevan and Sutherland 1991) method of multiple regression was used to jointly compare all possible models and identify variables that are independently correlated with species distribution responses. The leaps version 2.7 package in 'R' was used, for which computation is relatively quick because the method uses a branch and bound (Hocking and Leslie 1967) or leap and bound algorithm (Furnival and Wilson 1974; Lawler and Wood 1966) to calculate the residual sums of squares so that every set does not need to be considered. The programme computes a maximum of 31 variables at a time, however, the number of variables must be less than the number of observations otherwise the lower bound is uniformatively close to zero. The default options for selection of models that assume there is a linear, Gaussian model, are R^2, adjusted R^2 or Mallows C_p. The program was modified to use a non-parametric cross-validation PRESS (prediction sum of squares) statistic (Allen 1974; Miller 1990).

4.3.1 Spatial variation

The influence of geographic distance between sites on similarity of assemblages, referred to as autocorrelation, was investigated using the Mantel test in the Vegan package (Oksanen *et al*. 2007) in 'R' which for which Spearman's rank correlation for non-parametric data was used. The distances between a Bray-Curtis matrix of dissimilarity in species abundance for pairs of sites and a second matrix of geographic distances between pairs of sites were compared. The null hypothesis was that the distribution of one matrix was independent of the components of the other. A Monte Carlo permutation test for significance of the correlations calculated a statistic for the frequency of randomised correlations that were at least as strong as the observed correlations. A lower test statistic was more significant i.e. the distribution of one matrix was independent of the other which means that sites located closer together were not more similar than sites located further apart.

It must be noted, however, that the Mantel test used in this way is not suitable for questions about the raw data because it partitions the variation in a dissimilarity matrix. Variation of the dissimilarity (sums of squares) of a distance matrix is not a measure of beta diversity of the species among sites (Legendre *et al*. 2005). For this reason canonical analyses which partition the variation in species abundance data are able to explain a greater amount of total variation than the Mantel test which can only be applied to variation in groups of sites. Canonical analyses were therefore adopted for an examination of distance by partitioning variation as used by Borcard 1992; Cushman and Wallin 2002; Okland and Eilersten 1994; Oliver *et al*. 2000.

4.3.1 How much of the environmental and spatial variation explain species distributions?

Having identified spatial and environmental factors that corresponded to species distributions, it was possible to explore the amount of variation explained by each data matrix through partitioning of variation using partial canonical ordination. The method has been used to study assemblages of ants (Debuse *et al*. 2007), orbatid mites (Borcard and Legendre 1994) and plants (Ohmann and Spies 1998). Partitioned components were: environmental, spatial, the spatial component of environmental variation and undetermined.

Canonical correspondence analysis (CCA) combines multivariate ordination and simple multiple regression. The species ordination axes are constrained to be linear combinations of the environmental variables of the second matrix to provide an optimal relationship between the two.

CCA was first run with all environmental variables, then with partitioning of variation. Steps in the process are based on Anderson and Gribble (1998), Legendre and Legendre (1998) and Borcard *et al.* (2004).

Three matrices were required for the analysis, the first being a species matrix where species with an overall abundance less than 5 had been removed. Secondly a matrix

of a reduced number of environmental variables was necessary for Canonical Correspondence Analysis which is a constrained ordination. Redundant variables had been identified in earlier analyses such as NMDS, CAP and BIOENV and could further be identified through multiple regression using a forward stepwise selection procedure. It was also necessary to remove correlated variables.

The third was a Principal Coordinates of Neighbour Matrices (PCNM) matrix representing spatial variation of the species data (Dray *et al*. 2006). A PCNM was selected for modelling spatial components of variation in preference to a trend surface polynomial function of the centred coordinates of sites. PCNM has been found to provide a more realistic representation of the spatial components of species variation (Borcard 2002) and also enables this variation to be represented at different scales (Borcard and Legendre, 2004). This was an important consideration in this research for which species data were collected across two different scales. In addition, environmental variables that are categorical and therefore not additive, such as Braun-Blanquet scores of vegetation cover and aspect are not well represented by trend surface analysis which develops an area-wide regression model from which the values of variables at particular locations are predicted. Higher degree polynomials may be more representative of spatial complexity but reduce the degrees of freedom of the model (Legendre and Legendre 1998).

PCNM variables are principal coordinates of a truncated matrix of geographic (Euclidean) distances. The matrix of PCNM variables was created from a file of Cartesian coordinates (eastings and northings) using Spacemaker2 (Borcard *et al.* 2004), an open source programme available on the web from http://www.bio.umontreal.ca/legendre. Creation of a truncated matrix required input of the smallest truncation distance that would be large enough to join all sites. Relative neighbourhood graphs produce a minimal number of edges when connecting all points and were the graphing method used in R (version 2.4.1) to determine the truncation distance of 431 m which became the finest scale at which PCNM analysis could analyse the data. If desired, the analysis could be rerun at a finer scale by adding supplementary data points. The maximum distance across the whole study area was 1757 m, and this set the limit for the largest scaled PCNM variable's

wavelength.

The Spacemaker2 programme created the truncated distance matrix in which distances greater than the input value of 431 m were transformed to 1724 (= 4 x 431) and truncated. The truncated distance matrix was subjected to Principal Coordinates Analysis. The resulting set of principal coordinates which had positive eigenvalues became the set of PCNM variables available for modelling to analyse the response variables in regression or canonical analysis.

CCA of the three matrices was undertaken in R using the varpart function in the Vegan package (Oksanen *et al*. 2007). Species data were Hellinger transformed which is the square root of the ratio of the abundance of a species at a site to the total abundance at that site. This transformation has been shown to be suitable for canonical ordinations (Legendre and Gallagher 2001).

CCA of all variables, followed by successive partitioning resulted in identification of the contribution of spatial, environmental and unknown variables to the variation in species assemblages.

Explanatory tables:
X1: Environmental varaibles.
X2: Spatial variables
X3 Vegetation species

No. of explanatory tables: 2
Total variation (SS): 11.409
Variance: 0.49605
No. of observations: 24

Partition table:

	Df	R.squared
[a+b] = X1	23	1.00000
[b+c] = X2	16	0.73508
[a+b+c] = X1+X2	23	1.00000
Individual fractions		
[a] = X1|X2	7	
[b]	0	
[c] = X2|X1	0	
[d] = Residuals		

	Adj.R.squared
[a+b] = X1	
[b+c] = X2	0.12955
[a+b+c] = X1+X2	
Individual fractions	

[a] = X1|X2	
[b]	
[c] = X2|X1	
[d] = Residuals	
	Testable
[a+b] = X1	TRUE
[b+c] = X2	TRUE
[a+b+c] = X1+X2	TRUE
Individual fractions	
[a] = X1|X2	TRUE
[b]	FALSE
[c] = X2|X1	FALSE
[d] = Residuals	FALSE

Table 2.3 Example of labelling of partial variation for an environmental variables matrix, X1 and spatial variables matrix X2.

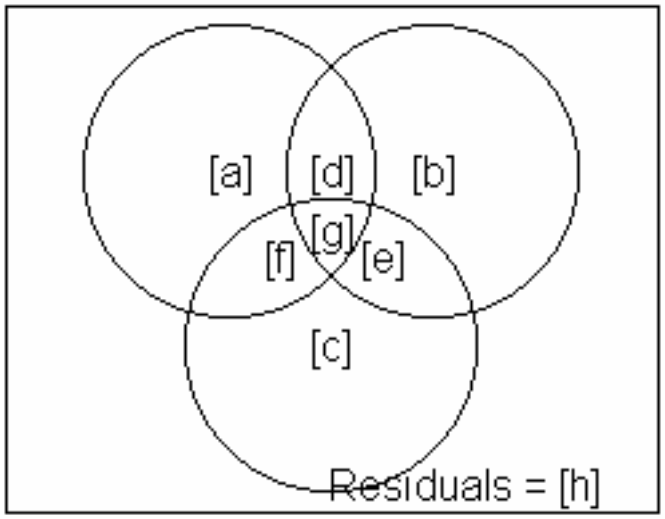


Figure 2.7 Diagram of how the partitioned variation of species assemblages with two explanatory matrices is labelled for use with the previous table. Each letter refers to a partial value of variation.

4.3.1 Particular species that correspond to forest type

A CAP analysis was used to find out whether particular species are associated with particular types of forest. This time Discriminant Analysis (DA) was used because only the species matrix was analysed, with species grouped by forest type to test for an effect of forest type grouping on the response matrix of species variables. The eigenanalysis was conducted as previously but this time the number of axes

explaining the most variation was tested by a criterion of minimum misclassification error with a cross-validation leave-one-out allocation of observations to groups (Anderson 2004).

Indicator Species Analysis (McCune and Grace 2002) was available with the PCORD programme. An Indicator Value (IV) for each species in each group was calculated to indicate how well each species separates among groups. Species with an abundance less than 5 overall were removed before analysis. The indicator value was the product of the proportional abundance of a species relative to its abundance in all forest types; and its proportional frequency in each forest type (number of forest types in which it was found), expressed as a percentage. Higher indicator values were stronger indicators. The null hypothesis tested was that the maximum indicator value for a species is no larger than would be expected by chance (i.e. zero). A Monte Carlo randomisation method was used to shuffle samples and recalculate the maximum indicator value for each species. The number of times the maximum indicator value was greater than the observed value was recorded, with low values being more significant.

Saragus costatus
(Tenebrionidae)

Chapter 3 Results

4.1 Abiotic variables

4.4.1 Altitude

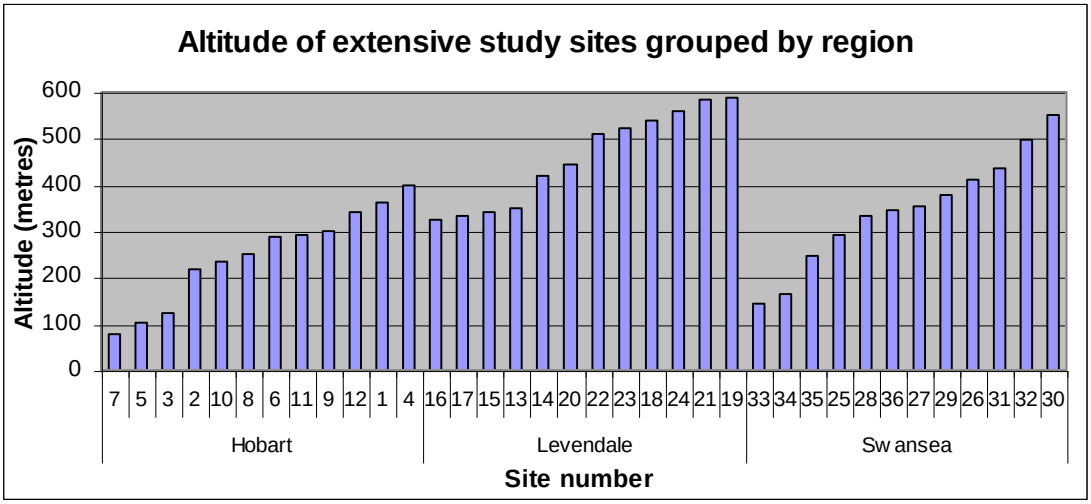


Figure 3.1 Regional variation in altitude of sites

All sites in the Mt Wellington study were in adjacent forest patches in the foothills, within 120 m altitude of each other. Their altitude ranged from 220 m (site 8) to 340 m (site 2). For the extensive survey the range in altitude was much greater, ranging from 78 m in the Hobart region (site 7) to 586 m in the Levendale region (site 19) (Figure 0.1).

4.4.1 Aspect

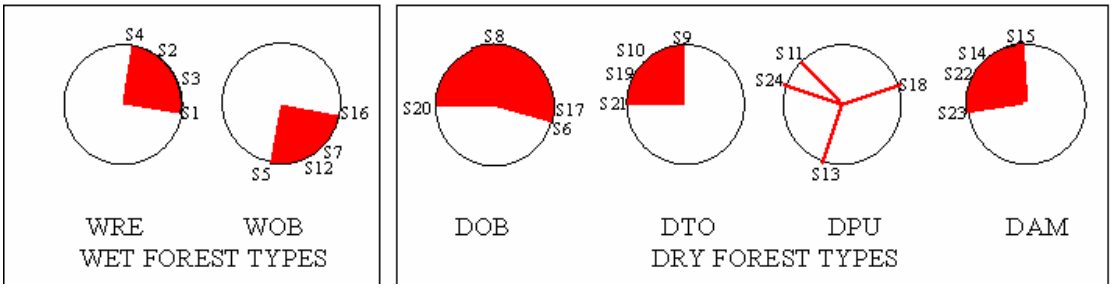


Figure 3.2 Range of aspect orientation of sites in each vegetation type in the Mt Wellington foothills.

General aspect orientation of sites in the different forest types in the Mt Wellington

foothills were quite distinctive, as displayed in Figure 3.2. For wetter forest types WRE sites generally faced NE and WOB sites had a SE aspect. DOB sites varied widely across northerly aspects while DTO and DAM sites generally faced NE. DPU sites varied considerably and it was difficult to generalise for this vegetation type.

4.4.1 Canopy cover and solar radiation

The percentage of canopy cover and solar radiation adjusted for canopy cover (see method section) is provided for each site in Table 3.1. Canopy cover was higher in wet WRE and WOB forests (65.94% - 83.3%) than in the drier DPU, DAM and DTO sites which had less than 50% cover (Figure 0.3). Canopy cover in DOB was about 55%.

	Canopy cover (%)	
Forest	mean	St. error
WRE	77.23	2.50
WOB	73.72	2.64
DOB	54.99	7.41
DPU	36.90	5.68
DAM	44.40	4.17
DTO	39.71	6.50

Table 3.1 Mean canopy cover in each forest type

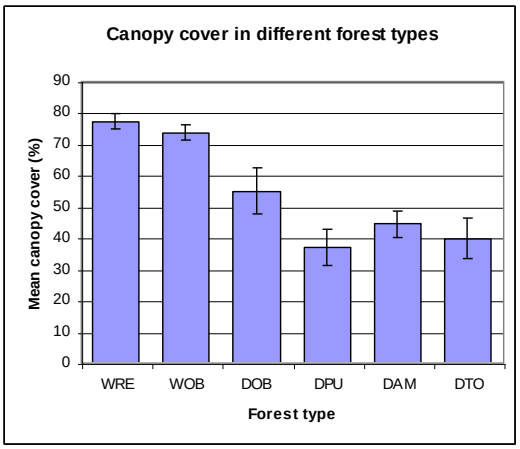


Figure 3.3 Mean canopy cover in each forest type

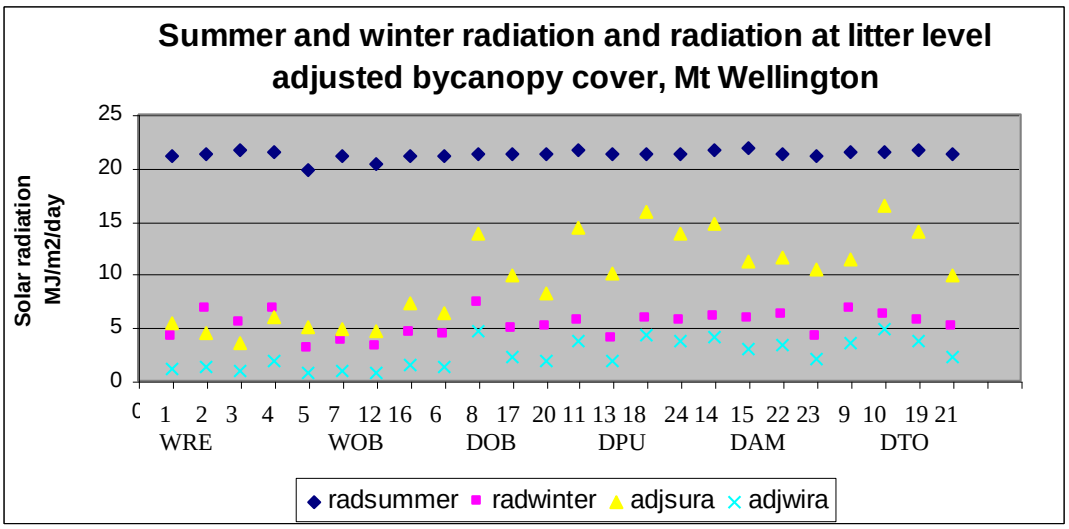


Figure 3.4 Summer and winter solar radiation at each site calculated from Nunez' model (1983) and accounting for aspect and slope. Adjusted radiation = solar radiation x (100 - % canopy cover)/100.

Summer solar radiation received on the sites was, overall, fairly constant due to the sun being high in the sky and unobstructed by topography. There was little difference between the minimum of 19.867 MJm^{-2}/day at site 5 and the maximum of 21.644 Mjm^{-2}/day at site 14. In winter the minimum insolent solar radiation was 2.922 MJm^{-2}/day at site 5 and maximum was 7.2MJm^{-2} at site 8 (Figure 3.4).

Adjusting solar radiation for canopy cover enabled an assessment of solar radiation received on the ground at the stratum of the litter invertebrates. Canopy cover reduced the impact of summer radiation in wetter forest types (WRE and WOB) to winter levels so there was little seasonal difference in solar radiation at wet sites. The more sparse canopy cover of drier forest types resulted in higher winter and summer radiation, with wider seasonal differences where canopy cover was lower.

4.4.1 Coarse Woody Debris (CWD)

Forest	Site	Vol CWD (m^3)	CWD hardness kgf/m^2
WRE	1	1.858	0.233
	2	0.673	0.533
	3	0	0
	4	0	0
WOB	5	3.821	0.090
	7	4.797	0.266
	12	12.89	0.55
	16	9.406	0.497
DOB	6	9.360	0.722
	17	0	0
	8	0.487261	1.75
	20	2.062	1.338
DPU	13	0	0
	18	0	0
	11	0.012	0.216
	24	0.759	1.066
DAM	14	0	0
	15	0.795	0.116
	22	0	0
	23	0	0
DTO	9	0.003	0.533
	10	0.093	0.1
	19	0	0
	21	0	0

Table 3.2 Volume of coarse woody debris > 5m diameter and its hardness measured at each site

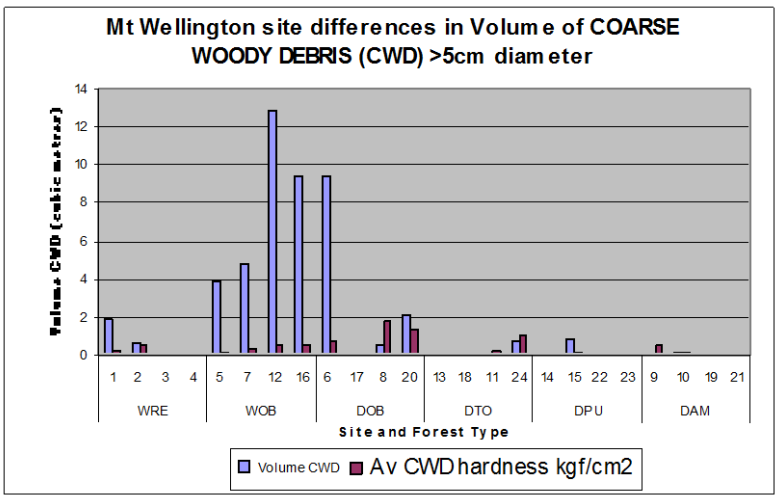


Figure 0.5 Variation of CWD (Coarse Woody Debris) and its hardness across sites in each forest type.

Results displayed in Figure 0.5 indicate that the four WOB sites (sites 5, 7, 12, 16) have an exceedingly high volume of CWD with a diameter greater than 5cm compared with sites in other forest types. CWD in wet WOB consisted of large rotting logs a metre or so in diameter and their measured hardness was low indicating they were soft due to advanced rot. In contrast there was a much smaller volume of CWD > 5cm in diameter in the drier sites and it was much harder, as indicated by the red bars in Figure 0.4. The CWD characteristics of one dry DOB forest site (site 6) mirrors those of wet WOB forest. This site was located between sites 5 and 7 on the same steep, south facing slope.

While WRE forest is also wet (sites 1, 2, 3, 4), it shares with the dry sites a low volume of CWD. Examination of sites 1 and 20 demonstrate a difference in the nature of the CWD, where it is hard in the dry site (site 20) and softer in the wet site (site 1).

4.4.1 Fungi

The volume of macro-fungi above ground varied considerably from site to site within each forest type even though it was collected on the same day (Table 3.3, Figures 0.5 and 0.6).

Veg type	av vol/veg	STAND ERROR
WRE	55.582	33.994
WOB	80.945	27.193
DOB	92.725	38.696
DTO	63.475	17.505
DPU	8.75	5.0087
DAM	21.925	19.02

Table 3.3 Average volume of fungi in each forest type and standard error

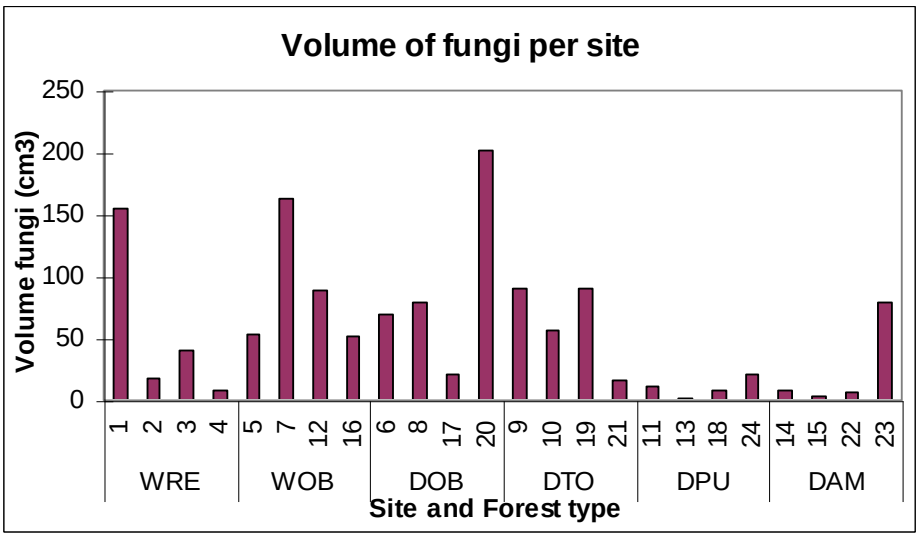


Figure 3.6 Volume of fungi at each site grouped by forest type

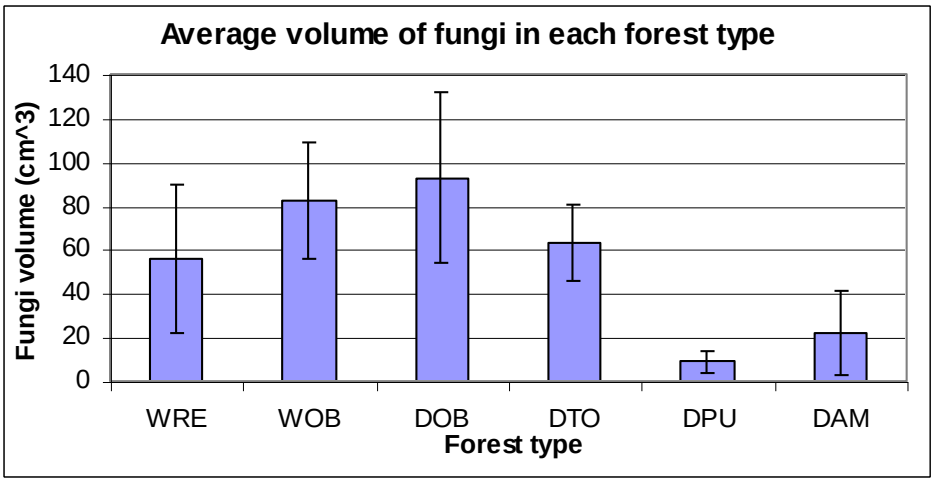


Figure 3.7 Average volume of fungi in each forest type with standard error indicated

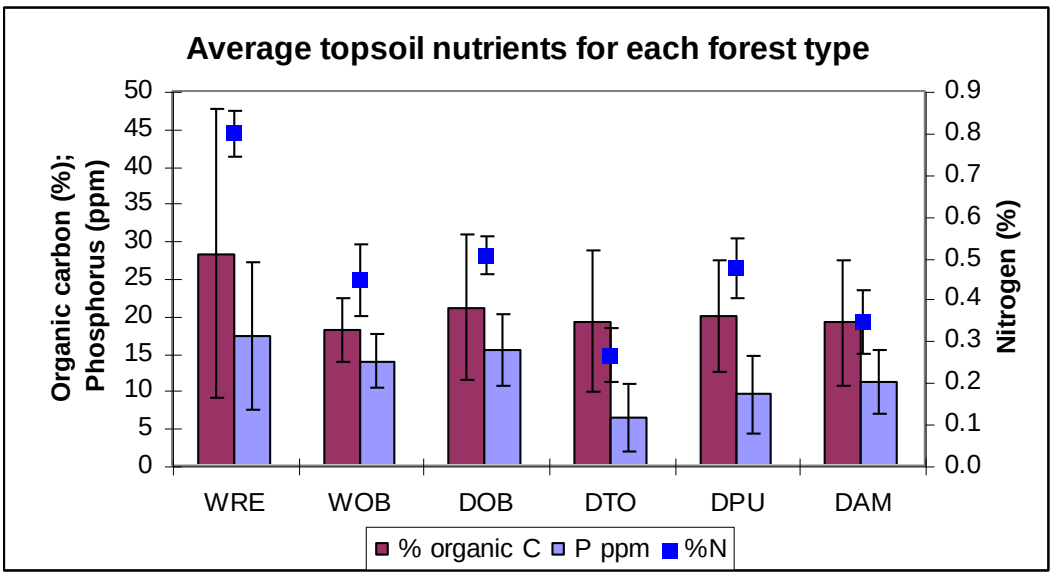
When grouped by forest type, fungi volume varied widely, as indicated by Figure 0.6 which displays the site variation, and by the large standard error for most forest types relative to the average volume (Figure 3.7).

4.4.1 Soil characteristics

Results of soil nutrient levels for each site can be found in Appendix 6 . Nutrient results (carbon, phosphorus and nitrogen) have been averaged for each vegetation type (Table 3.4) and are graphed below, (Figure 3.8), with error bars to represent standard error between sites.

Top soil nutrients – A horizon						
Forest	av org C %	av P ppm	av N %	st error org C	st error P	st error N
WRE	28.21	17.23	0.80	1.16	1.75	0.05
WOB	18.00	13.95	0.44	2.28	1.62	0.09
DOB	21.03	15.32	0.50	1.77	1.13	0.05
DTO	19.23	6.36	0.27	2.74	0.77	0.07
DPU	19.96	9.51	0.48	1.49	1.76	0.07
DAM	19.06	11.09	0.35	3.24	2.43	0.08
Subsoil nutrients to 10cm – B horizon						
	av org C	av P ppm	av N	st error org C	st error P	st errorv N
WRE	19.27	9.87	0.35	2.96	3.35	0.11
WOB	4.30	3.70	0.11	2.48	2.68	0.06
DOB	9.71	4.78	0.19	0.89	0.42	0.03
DTO	9.38	4.58	0.10	1.31	0.37	0.02
DPU	7.52	5.17	0.14	0.64	0.65	0.02
DAM	8.32	4.24	0.12	1.41	0.81	0.03

Table 3.4 Summary mean soil nutrients for topsoil and subsoil to 10cm depth.



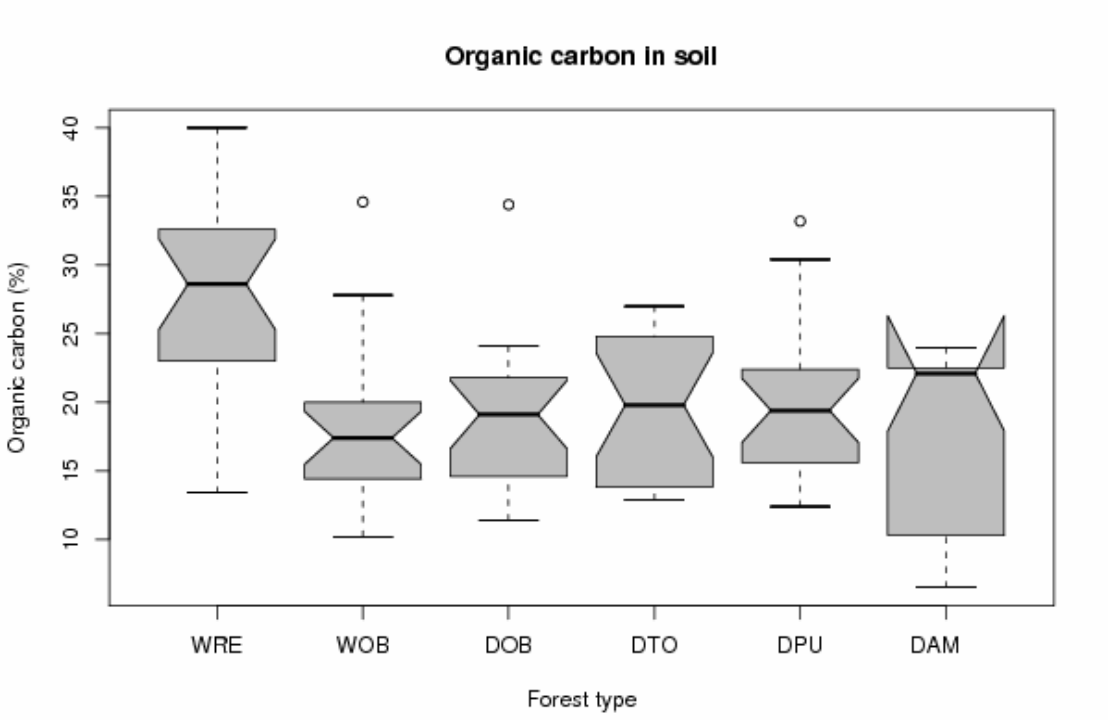


Figure 0.8 Average topsoil nutrients (% organic carbon, Phosphorus (ppm) and % Nitrogen) for each forest type with standard error bars indicating variation in the data at sites within each forest type (above), with a notched boxplot of organic carbon in the soil (below) to provide an example of the high variability of soil nutrients within the same forest types.

For the wet forest types, average organic carbon and Phosphorus levels were higher in WRE forest (28.21%; 17.23 ppm) than WOB wet forest (18%;13.95 ppm) (Figure 3.9). Average organic carbon levels were similar in each of the dry forest types (about 20%), while phosphorus varied from 15.32 ppm in dry DOB forest to 6.36 ppm in DTO forest. Nitrogen levels varied widely, being highest in WRE (DTO also displayed the lowest level of phosphorous (6.36 ppm) in any forest type, with WRE forest phosphorus levels highest at 28.21 ppm.

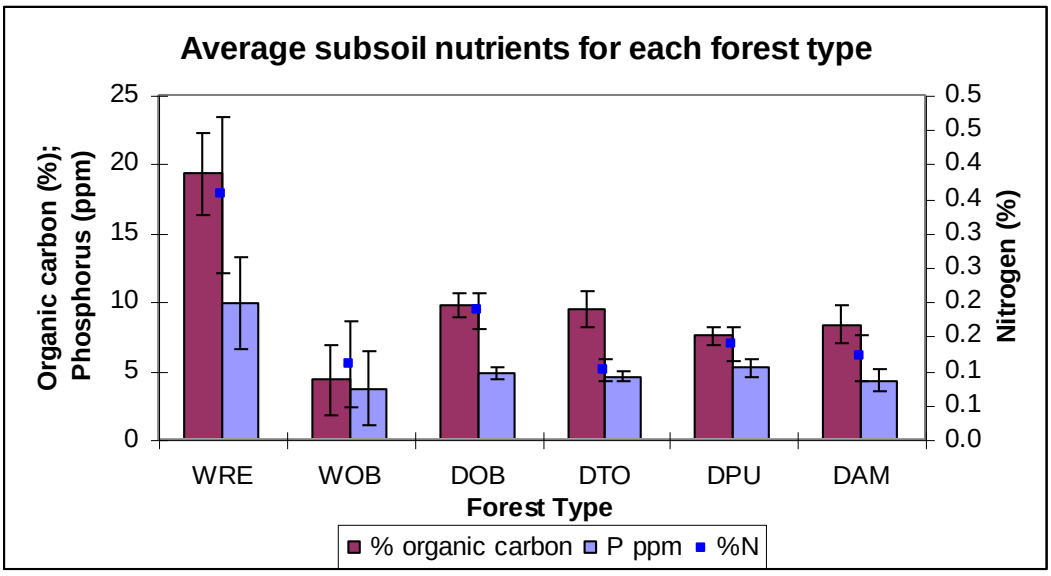


Figure 0.9 Average subsoil nutrients for each vegetation type with standard error bars indicating the variation in the data at sites within each forest type. Depth is to 10 cm.

Subsoil nutrients were all lower than the topsoil layer in nitrogen levels. Organic carbon and phosphorus was lower across all forest types, while DTO forest soil, which had the lowest organic layer nutrients, showed the same low levels of nutrients in the bottom layer.

4.1 Plant species

A full list of plant species identified for each site with assistance from Nicky Meeson and Professor Jamie Kirkpatrick is provided in Appendix 3 for Mt Wellington and regional sites.

4.1 Beetle Assemblages

4.6.1 Dominant beetle families sampled

A total of 1726 beetles representing 152 species from 28 families were collected during the intensive Mt Wellington study across 3 seasons (November 2002, February 2003 and April 2003).

Two genera were an order of magnitude more common – *Thalycrodes* spp. (Nitidulidae) with 586 individuals across all sites, and *Promecoderus* spp. (Carabidae) with 424 individuals.

FAMILY	GENUS (species)	NUMBER	PERCENT OF ALL BEETLES %
Nitidulidae	*Thalycrodes*	586	34
Carabidae	*Promecoderus*	424	24.6
Curculionidae	*Poropterus*	76	4.4
Leiodidae	*Nargomorphus*	55	3.2
Curculionidae	*Mandalotus* small narrow	24	1.4
Tenebrionidae	*Isopterum obscurum*	21	1.2
Tenebrionidae	*Saragus costatus*	20	1.2

Table 3.5 List of the most abundant beetle species at the Mt Wellington foothill sites

Table 3.6 displays the families in ranked order of abundance and includes the number of species in each family. These results are displayed in Figure 0.10.

RANK	FAMILY	# individuals	# species
1	Nitidulae	542	3
2	Carabidae	439	9
3	Staphylinidae	260	31
4	Curculionidae	145	23
5	Leiodidae	73	9
6	Scarabaeidae	68	14
7	Pselaphidae	53	15
8	Tenebrionidae	60	10
10	Elateridae	18	7
11	Latridiidae	15	3
12	Lucanidae	13	3
13	Chrysomelidae	12	5
14	Scydmaenidae	12	5
15	Ptilidae	7	2
16	Silvanidae	3	1
17	Melandryidae	2	2
18	Corylophidae	2	1
19	Eucinetidae	2	1
20	Melyridae	2	1
21	Sphindidae	1	1
22	Zopheridae	1	1
23	Anthicidae	1	1
24	Coccinellidae	1	1
25	Lycidae	1	1
26	Mordellidae	1	1
27	Oedemeridae	1	1
28	Cerambycidae	1	1

Table 3.6 Ranked abundance of beetle families trapped and number of species in each family.

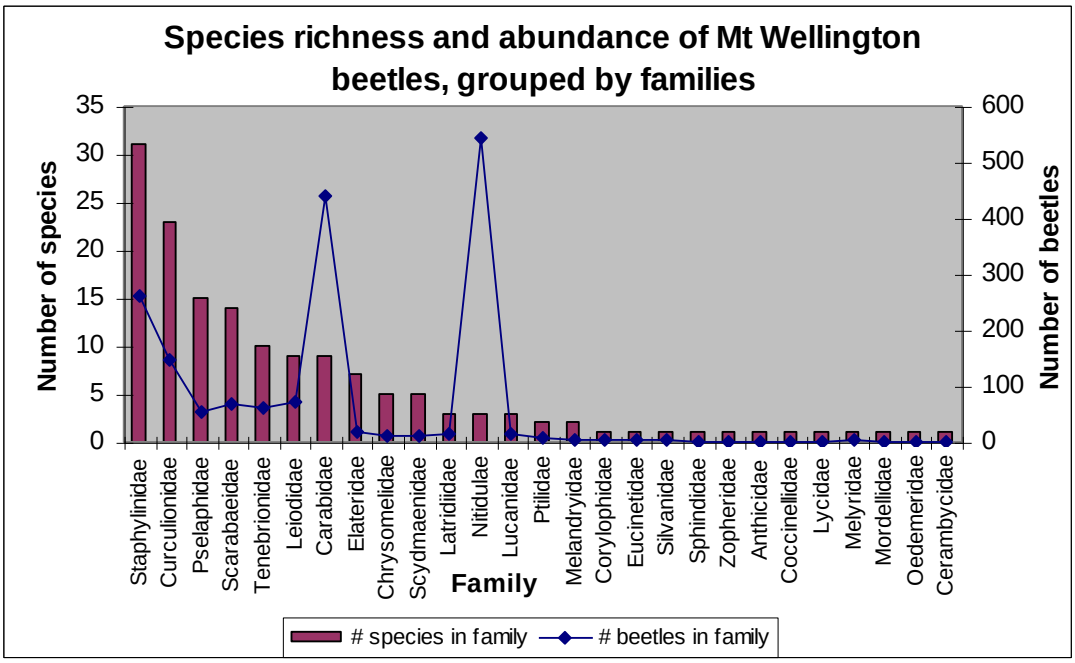


Figure 3.10 Beetle family richness at Mt Wellington sites with an overlay of the number of beetles in each family.

Figure 0.10 indicates that a few families are represented by a large number of species, the most dominant families being Staphylinidae, Curculionidae, Pselaphidae, Scarabaeidae, Leiodidae, Tenebrionidae and Carabidae. There is a long tail of families represented by only one or two species.

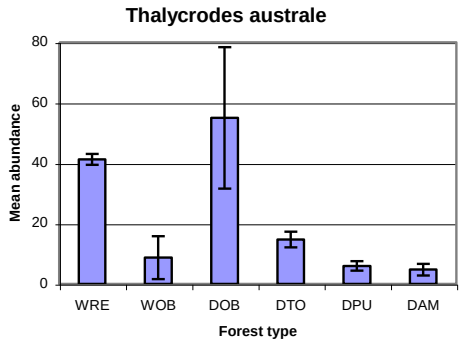
The number of beetles recorded from each family follows a general trend of decreasing adundance with decreasing number of species, but several families counter this trend, notably Nitidulae and Carabidae where the spikes in species numbers are attributable to a single species in each family - *Thalycrodes australe* (Germar, 1848) and *Promecoderus longus* (Sloane, 1920) respectively.

4.6.1 Overview of beetle families sampled

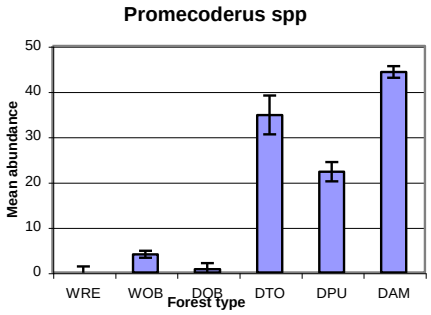
Members of only one genus from the Nitidulae family, *Thalycrodes,* was trapped but it was the most abundant of all beetles, with 586 specimens collected across most sites.

Beetles from the Carabidae family made up approximately a quarter of all beetles trapped (439 individuals), most of them being *Promocoderus* spp which were absent from the wet forest types, WRE and WOB. Other carabids occurred in small numbers. Twenty three species of Curculionidae were trapped in this study with most being from two main subfamilies: Entiminae (which includes the genus *Mandalotus*) and Cryptorhynchinae. Sixty-four beetles from the Leiodidae family were represented by three species: *Nargomorphus* sp., *Zeadolophus* sp. (4 individuals) and a specimen of *Eublackburniella* sp. Over half of the sixty-eight Scarabaeidae beetles collected were in the genus *Heteronyx.*

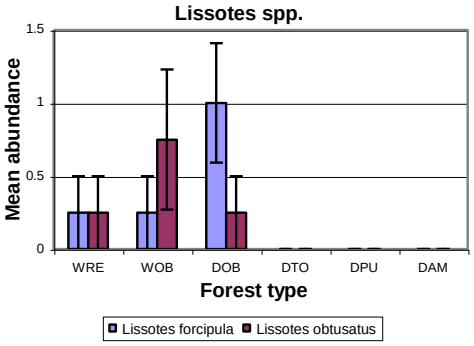
A single rare click beetle , *Parablax* sp. (Elateridae) not previously seen in Tasmania (McQuillan, pers.comm.) was collected in this study. The first record of the introduced dung beetle, *Euoniticellus* sp. (Scarabidae) in native habitat was recorded from a pitfall trap in *E. tenuiramis* forest type, in an area near several walking tracks. The distributions of some of the most abundant species among different forest types are portrayed in Figure 0.11.



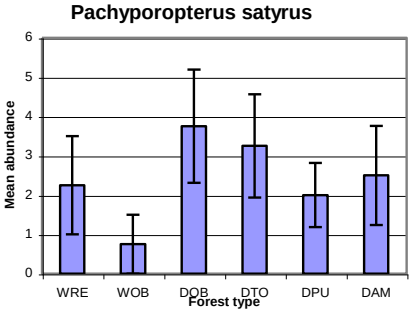
(a) *Thalycrodes australe* (Nitidulae)



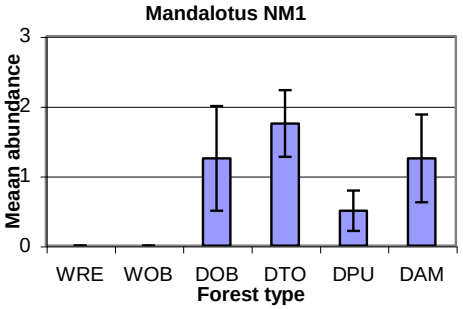
(b) *Promecoderus* spp. (Carabidae)



(c) *Lissotes forcipula* and *L. obtusatus* (Lucanidae)



(d) *Pachyporopterus satyrus* (Curculionidae)



(e) *Mandalotus* NM1 (Curculionoidae)

)

Figure 0.11 Graphs of mean abundance of common beetle species in different forest types.

4.6.1 Seasonal variation in distribution of beetles

Seasonal variation in occurrence of species was provided to assess interpretations of species presence and abundance from sampling of extensive sites in only one season.

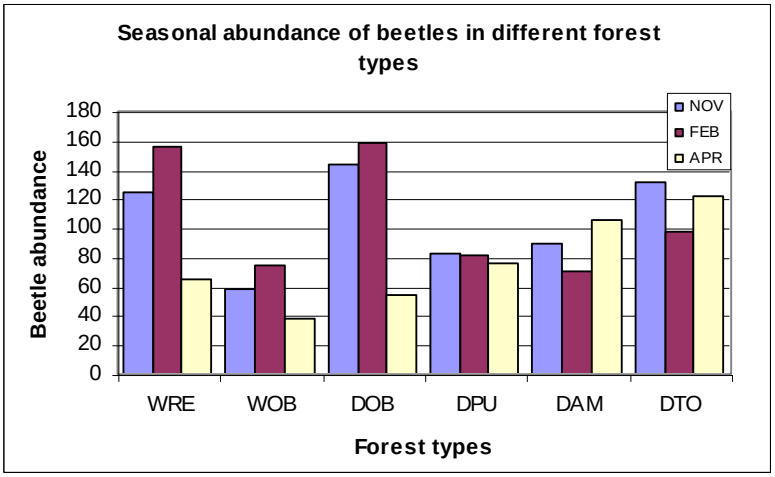
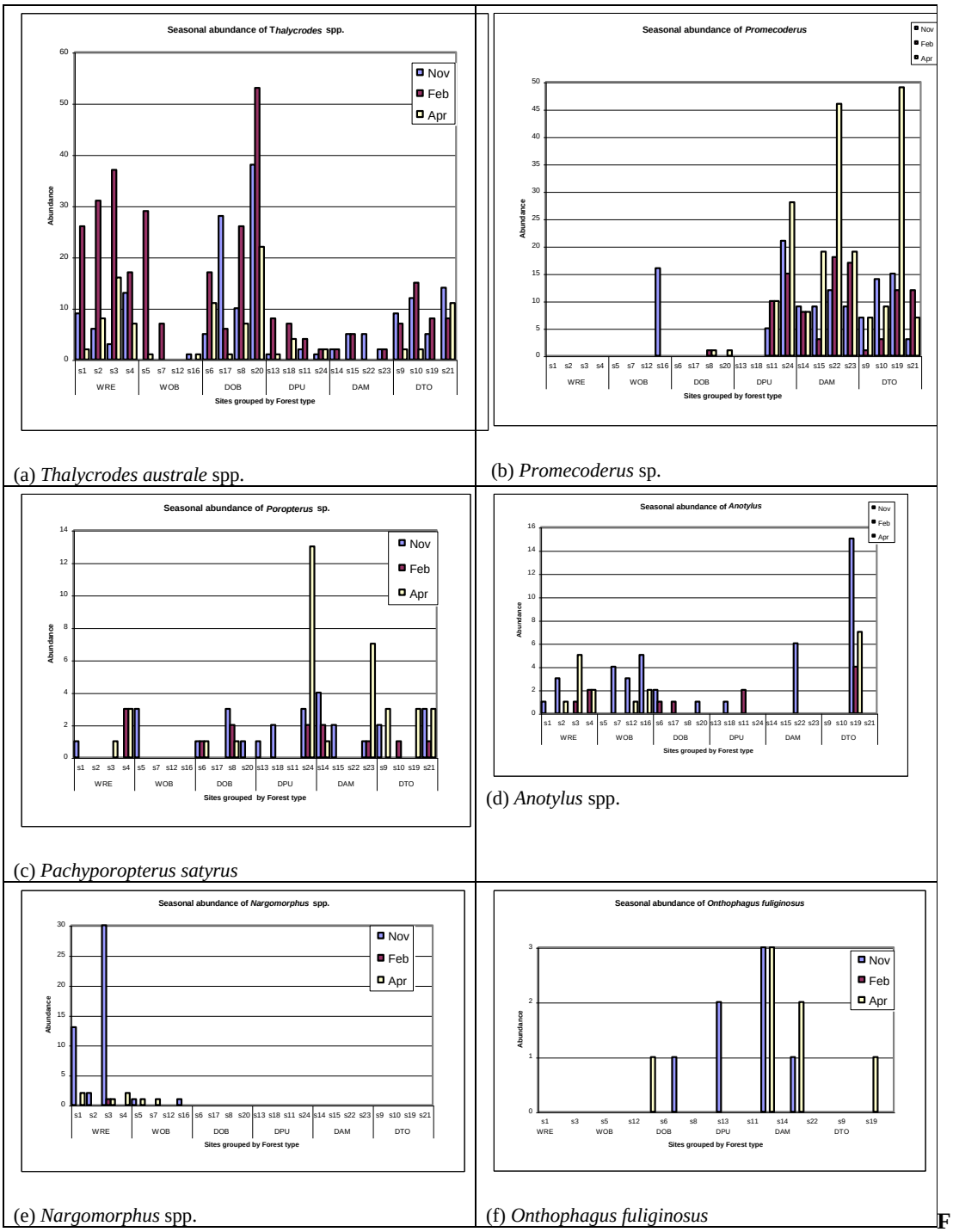


Figure 3.12 Seasonal abundance of beetles in different forest types from the Mt Wellington study.

Seasonal occurrence of beetles in the Mt Wellington foothills showed highest numbers in summer (February) in the wetter WRE and WOB forest types and DOB, with much lower numbers in autumn (April). There was little seasonal variation in DPU, while the dry DAM and DTO had slightly lower numbers in summer (February) than in other months.



(a) *Thalycrodes australe* spp.

(b) *Promecoderus* sp.

(c) *Pachyporopterus satyrus*

(d) *Anotylus* spp.

(e) *Nargomorphus* spp.

(f) *Onthophagus fuliginosus*

Figure 3.13 Seasonal occurrence of some of the sampled Mt Wellington beetles in different forest types in February, April and November.

Beetles varied seasonally in their abundances in different forest type (Figure 3.13). *Thalycrodes australe* (Germar, 1848) was generally present across all forest types but was particularly numerous in WRE and DOB in February. *Promecoderus* was

generally found in drier forest types with peak abundances in April. *Pachyporopterus satyrus* (Pascoe, 1872) was generally present across all forest types but its peak abundances occurred in April in DPU and DAM. *Onthophagus fuliginosus* Erichson, 1842 was absent from wet forest types and absent in November samples. In contrast, *Nargomorphus* spp. were confined to wetter sites with peak abundances in November. *Aridius minor* (Blackburn, 1888) and *Mandalotus* NM3 were absent from DPU with *Aridius minor* (Blackburn, 1888) showing a peak abundance at a single site in November and *Mandalotus* NM3 with higher abundances in November and February than in April.

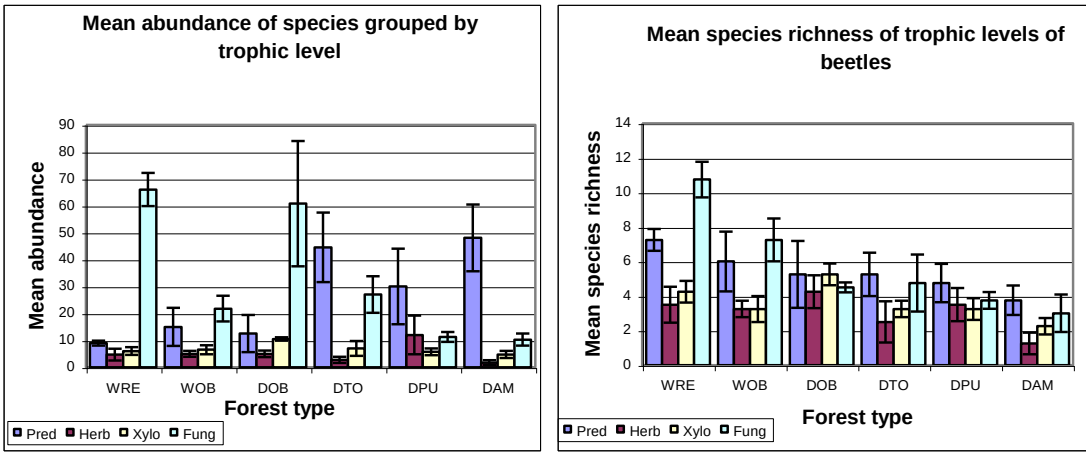
4.6.1 Trophic levels of beetles

	Mean abundance							
Forest	**Pred**	**st. error**	**Herb**	**st. error**	**Xylo**	**st. error**	**Fung**	**st. error**
WRE	9	0.912	4.75	2.174	6	1.414	66	6.164
WOB	15	7.011	5	1.080	6.5	1.707	21.75	4.767
DOB	12.5	6.885	5	1.224	10.5	0.645	60.75	23.23
DTO	44.5	12.92	2.75	1.181	7	2.798	27	6.757
DPU	30	13.97	12	7.153	5.75	1.314	11.25	1.796
DAM	48	12.41	1.75	0.853	4.75	1.314	10.25	2.25

	Mean species richness							
Forest	**Pred**	**st. error**	**Herb**	**st. error**	**Xylo**	**st. error**	**Fung**	**st. error**
WRE	7.25	0.629	3.5	1.040	4.25	0.629	10.75	1.030
WOB	6	1.732	3.25	0.478	3.25	0.75	7.25	1.25
DOB	5.25	1.931	4.25	0.946	5.25	0.629	4.5	0.288
DTO	5.25	1.25	2.5	1.190	3.25	0.478	4.75	1.652
DPU	4.75	1.108	3.5	0.957	3.25	0.629	3.75	0.478
DAM	3.75	0.853	1.25	0.629	2.25	0.478	3	1.080

Table 3.7 Mean abundance and mean species richness of beetles grouped by trophic level in

different forest types. Pred = predator, Herb = herbivore, Xylo = xylophage and Fung = fungivores and saprophages.



(a) (b)

Figure 3.14 (a) Mean abundance of beetle species grouped by trophic level. (b) Mean species richness of beetles grouped by trophic level. Pred = predator, Herb = herbivore, Xylo = xylophage and Fung = fungivores and saprophages.

Fungivorous beetles outnumbered predators in wet forest types and DOB while predators were the most numerous in dry forests DTO, DAM and DPU (Figure 3.14 a). Fungivores were more species rich in wet forest types while predators were slightly more species rich in dry forest types (Figure 3.14 b).

4.1 Spider assemblages

4.7.1 Dominant spider families sampled

A total of 1983 adult and juvenile spiders representing 204 species from 20 families were sampled at the Mt Wellington sites. Adult spiders alone totalled 1302 individuals representing 187 species/morphospecies from the same 20 families. The additional

17 families created from inclusion of juveniles is a possible source of error due to incorrect identification when calculating diversity. Each of those extra families was only represented by an abundance of one or two individuals and was excluded from analyses where rare species (represented by less than five individuals) are first excluded. The families in the Mt Wellington data that included morphospecies of only juveniles were Clubionidae and Theridiidae with one extra species, Salticidae, Thomisidae, Gnaphosidae, Zodariidae and Zoridae with 2 extra species and Linyphiidae with 5 extra species.

The dominant spider family in terms of abundance was the web builder, Linyphiidae with 315 individuals from 28 species. The next six dominant families were vagrant hunters: Lycosidae, Corrinidae, Gnaphosidae, Amaurobiidae, Zoridae, and Zodariidae (Table 3.8).

Spiders (adults)			
Rank	Family	# individuals	# species
1	LINYPHYIDAE	315	28
2	LYCOSIDAE	300	13
3	CORRINIDAE	255	5
4	GNAPHOSIDAE	182	30
5	AMAUROBIIDAE	138	17
6	ZORIDAE	88	10
7	ZODARIIDAE	70	21
8	THERIDIIDAE	33	11
9	SALTICIDAE	24	18
10	SEGESTRIIDAE	21	2
11	MICROPHOLCOMMATIDAE	13	4
12	NICODAEMIDAE	13	3
13	MYGALOMORPHIDAE	9	4
14	CLUBIONIDAE	4	1
15	MIMMETIDAE	3	3
16	THOMISIDAE	2	4
17	ANAPIDAE	1	3
18	CTENIDAE	1	2
19	GNAPHOSOIDIAE	1	1
20	HAHNIIDAE	1	2

Table 3.8 Ranked order of abundance of adult spider families, including species richness of each family.

A list of species/ morphospecies of spiders appears in Appendix 4.

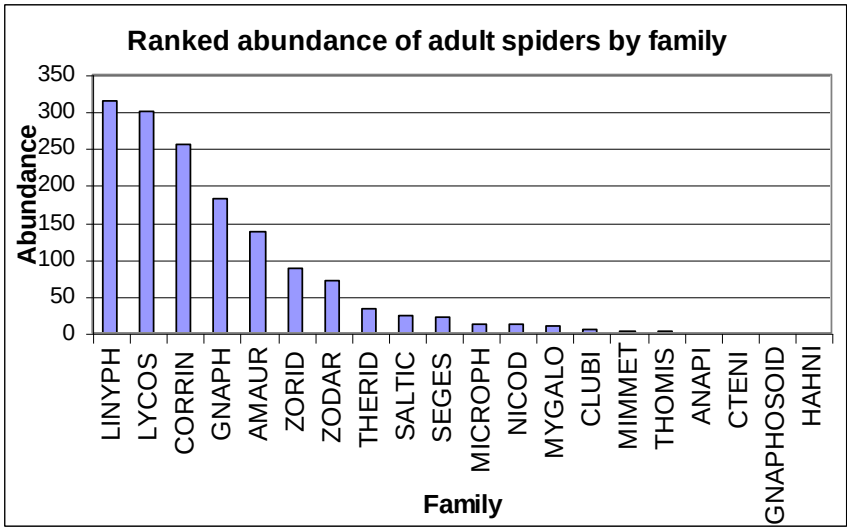


Figure 3.15 Graphed rank abundance of adult spider families

Spiders (Adults) Family	Species code	Ranked Abundance	% of all spiders	Hunting style
Corrinidae	SUPPNM1	217	17	vagrant
Linyphiidae	LINYDICR	193	15	web
Lycosidae	LYCART1	142	11	vagrant
Linyphiidae	LINYDIP1	58	4	web
Zoridae	ZORHESA	37	3	vagrant
Gnaphosidae	GNAPNM16	22	2	vagrant
Linyphiidae	LINYNM19	21	2	web
Zodariidae	ZODNM12	18	1	vagrant
Gnaphosidae	GNAPNM23	17	1	vagrant
Linyphiidae	LINYLAE1	17	1	web
Micropholcommatidae	MICNM1	16	1	web
Amaurobiidae	AMAUNM2	15	1	web
Gnaphosidae	GNAPNM15	15	1	vagrant
Gnaphosidae	GNAPNM36	15	1	vagrant
Gnaphosidae	GNAPNM1	14	1	vagrant
Gnaphosidae	GNALNM28	14	1	vagrant
Zodariidae	ZODSTFL	14	1	vagrant
Zoridae	ZORNM4	13	1	vagrant
Amaurobiidae	AMAUNM6	12	1	web
Segestriidae	SEGARIAD	12	1	vagrant
Gnaphosidae	GNAPNM22	11	1	vagrant
Zodariidae	ZODNM25	11	1	vagrant
Gnaphosidae	GNAPNM2	10	1	vagrant
Theridiidae	THERDIP1	10	1	web
Amaurobiidae	AMAUNM8	9	1	web
Lycosidae	LYCART6	9	1	vagrant
Theridiidae	THERACH	9	1	web

Gnaphosidae	GNAPNM13	8	1	vagrant
Gnaphosidae	GNAPNM17	8	1	vagrant
Amaurobiidae	AMAUNM3	7	1	web
Gnaphosidae	GNAPNM3	7	1	vagrant
Lycosidae	LYCVENPI	7	1	vagrant
Lycosidae	LYCNM1	7	1	vagrant
Salticidae	SALTNM4	7	1	vagrant
Mygalomorphae	MYGATRA	7	1	vagrant
Gnaphosidae	GNAPNM4	6	<1	vagrant
Linyphiidae	LINYLIN1	6	<1	web
Lycosidae	LYCTROC2	6	<1	vagrant
Nicodaemidae	NICNOVNO	6	<1	web
Gnaphosidae	GNAPNM14	5	<1	vagrant
Lycosidae	LYCART5	5	<1	vagrant
Lycosidae	LYCART8	5	<1	vagrant
Micropholcommatidae	MICLONG	5	<1	web
Micropholcommatidae	MICTEXN1	5	<1	web
Amaurobiidae	AMAUNM1	4	<1	web

Table 3.9 Ranked abundance of spider species sampled with abundance > 4 at Mt Wellington.

Table 3.9 ranks spider species sampled at Mt Wellington. A further 142 species with abundance less than 5 across all sites have been excluded. The abundances of the dominant 35 species are displayed in Figure 3.16.

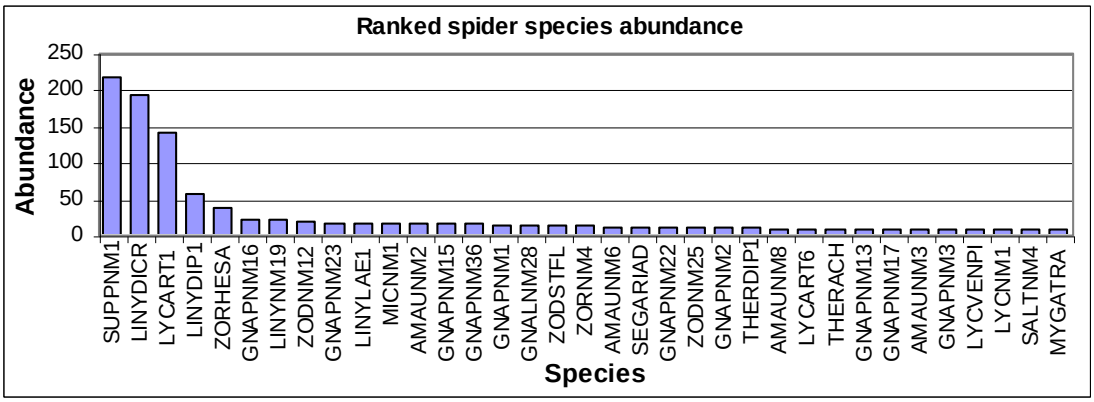


Figure 3.16 Graph of ranked abundance of the dominant 35 spider species sampled at Mt Wellington sites.

4.7.1 Seasonal variation in distribution of spiders

The number of spiders and the number of active species varied seasonally (Figure 3.17).

In drier forests (DOB, DTO, DPU and DAM), species abundance was highest in November, whereas in wetter forests (WRE and WOB) seasonal abundances were lower, with a general trend for slightly more spiders in February than November. This pattern was similar for species richness.

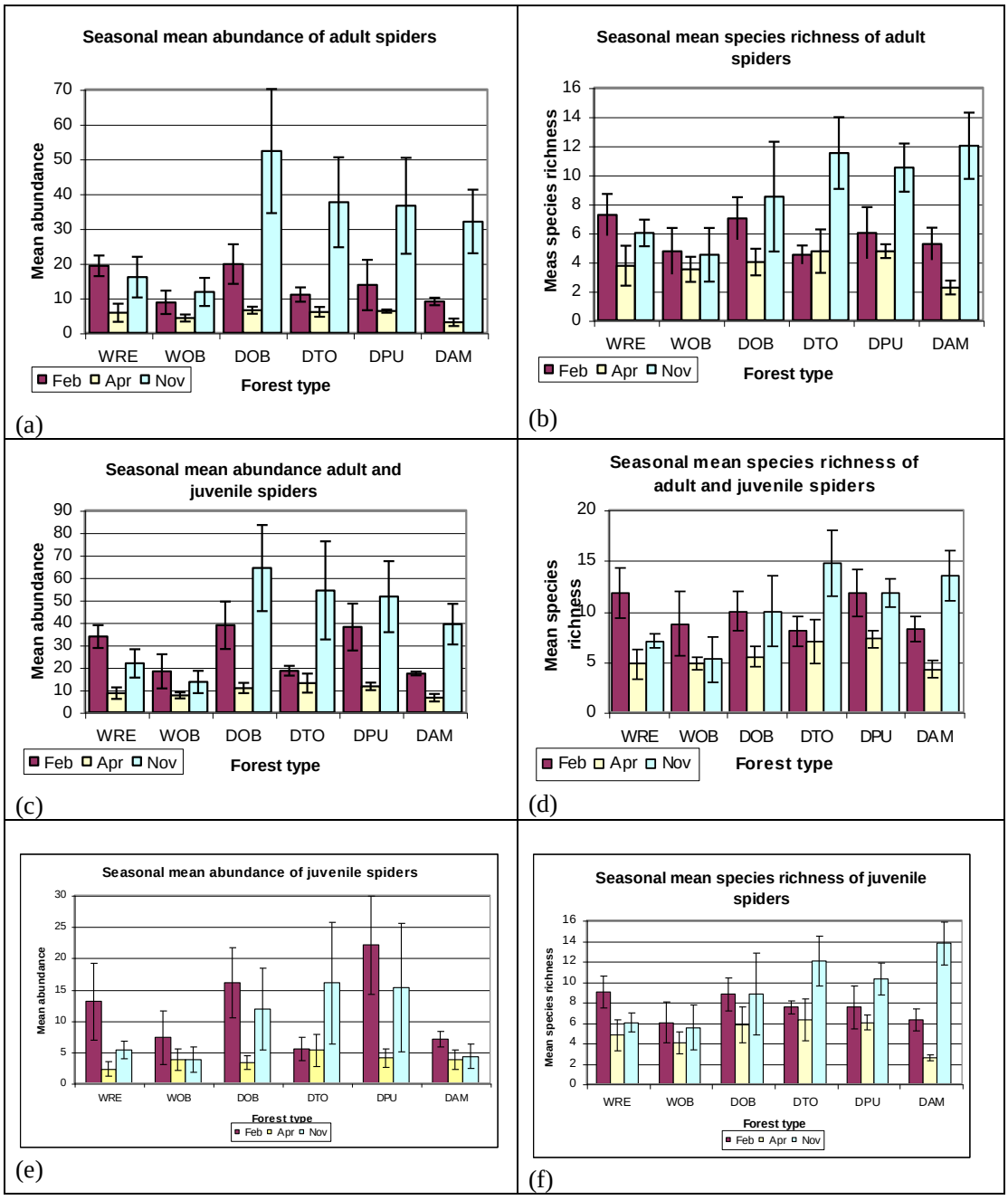


Figure 3.17 Seasonal abundance and species richness of adult and juvenile spiders in different forest types.

Figure 3.18 provides some typical examples of the seasonal distribution of spider species in different forest types. Generally species were present at dry forest sites or wet forest sites, but all showed a large variation within each forest type, as

indicated by large error bars, which suggests that being grouped by forest type was highly variable. Few were active in April. The seasonal patterns of juvenile spiders mirror those of adults in wet forest types and DTO but show an inverse pattern in other dry forest types where their abundance decreases in summer to lower than spring levels.

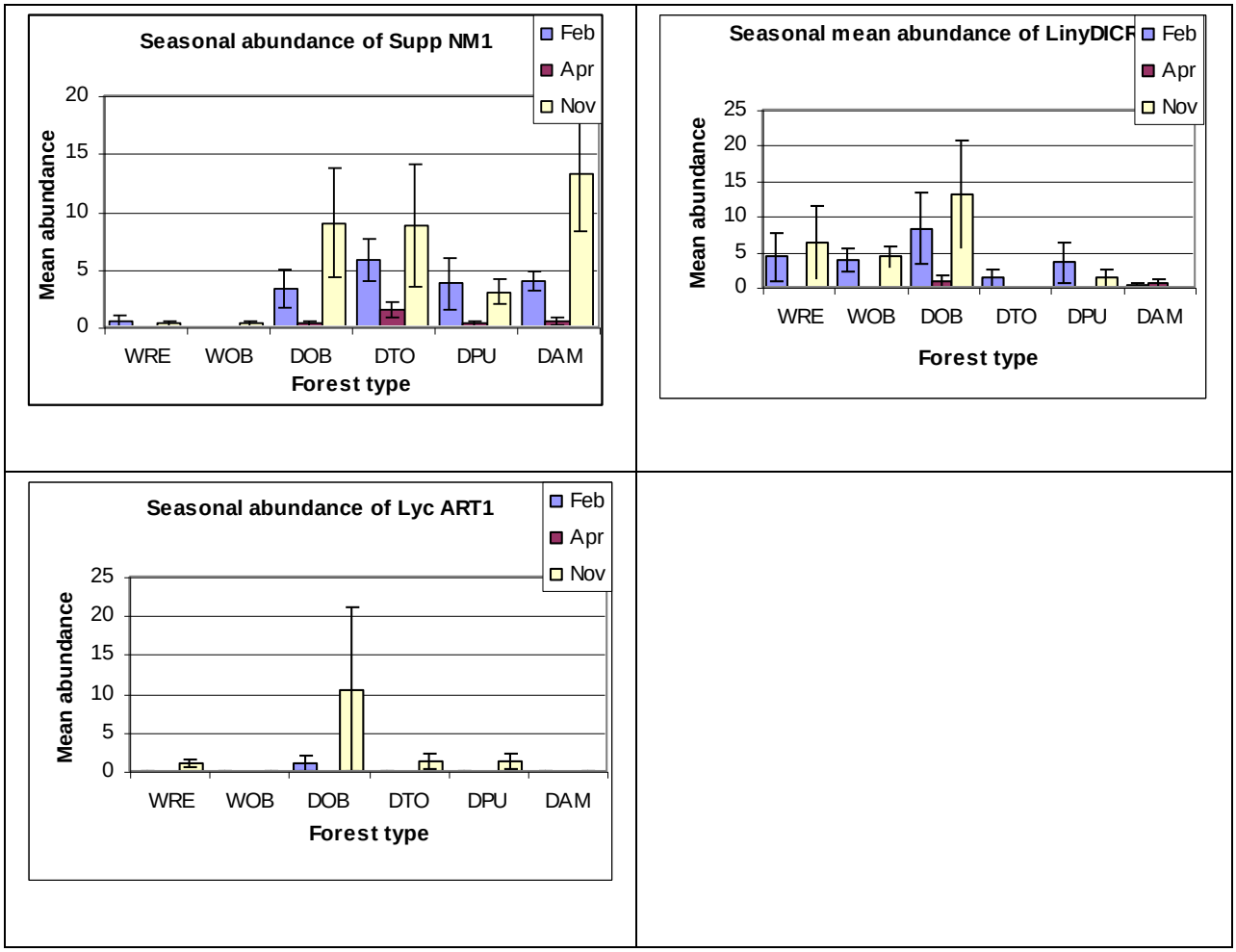


Figure 3.18 Seasonal abundance of some spiders in different forest types: *Suppuna* NM1 (Corrinidae), *Diplocephalus cristatus* (Linyphiidae) and *Artoria* NM1 (Lycosidae).

4.7.1 Distributions of spiders with different hunting styles

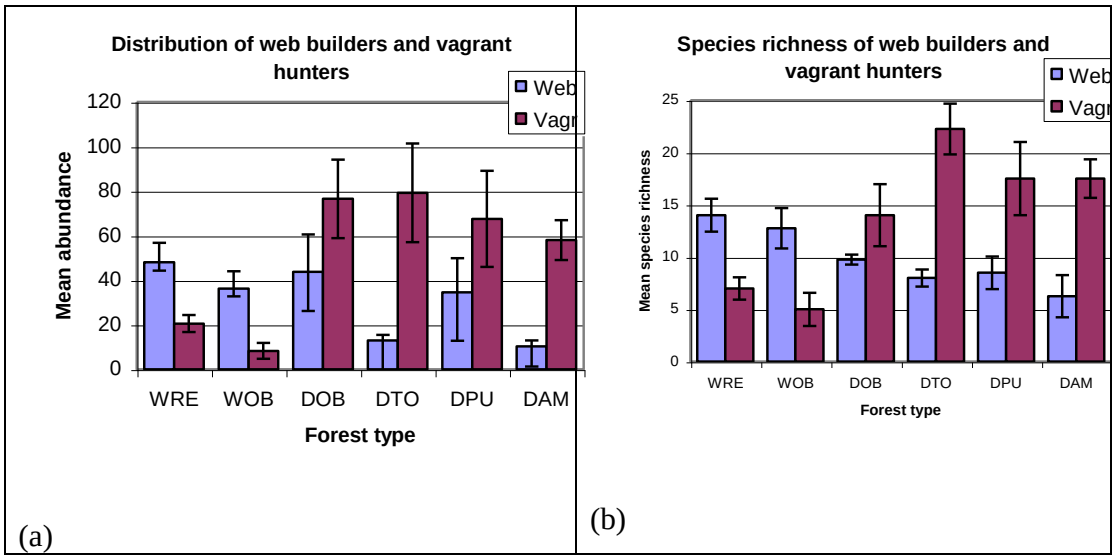


Figure 3.19 Mean abundance (a), and species richness (b), of web builders and vagrant hunters in different forest types.

Web building dominated the numbers and species richness of spiders in wet forest types. Vagrant hunters were dominant in abundance and species richness in the drier forest types (Figure 3.19).

4.1 Statistical Analysis of data

4.8.1 Beta diversity

Species abundance and richness varied between forest types (Figure 3.20).

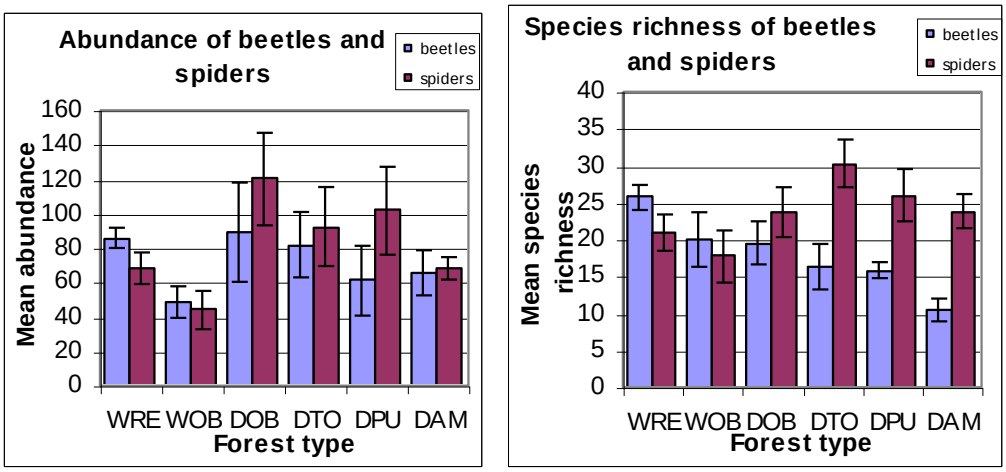


Figure 3.20 Comparison of beetle and spider abundance and species richness in different forest types.

Dry forest types (WOB, DTO, DPU and DAM) contained more spiders than beetles and a greater diversity of spiders. The opposite was observed in wet forests (WRE and WOB) where beetles dominated spiders in diversity and abundance.

4.8.1.1 Local variation

Local variation in beta diversity for different taxa among adjacent forest types is compared in Table 3.10 using a modified Whittaker's index for beta diversity (Harrison *et al.* 1992).

		Spp Rich-ness	β–diversity indices						overal l β
			Forest type						
			WRE	WOB	DOB	DTO	DPU	DAM	
Modified Whittaker's Index	Vascular plants	147	22.83	18.26	7.43	12.53	7.52	8.19	7.43
	Beetles	152	24.48	22.79	26.43	28.73	38.87	50.84	24.48
	Spiders (all)	204	34.11	36.96	28.61	24.64	28.61	31.68	28.61
	Spiders (adults)	187	45.17	45.17	28.04	29.04	31.27	35.35	29.04
	Fungi	64	23.19	14.65	27.83	46.38	139.13	69.57	14.65

Table 3.10 Whittaker's Index for beta diversity, modified by Harrison *et al.* (1992) for the Mt Wellington species. Sampling occurred in February, April and November.

The degree to which sites in one forest type shares species with sites in another forest type is referred to as species turnover (Oliver *et al*. 1998). Species turnover was lower (more species in common) for vascular plants than invertebrates, indicating that sites within the same forest types generally shared the same plant species. The drier forest types (DOB, DTO, DPU and DAM) had the lowest plant species turnover (beta diversity lowest in DOB and DPU at 7.43 and 7.52 respectively). Conversely, beetles had highest species turnover between sites within two of the drier forest types (DPU and DAM with beta diversity 38.87 and 50.84 respectively). Adult spiders showed highest species turnover among wet forest types (WRE and WOB with beta diversity 45.17 for each). Fungi demonstrated exceptionally high species turnover among drier forest types.

It should be noted, that unlike plants, repeated sampling for fungi will continue to reveal new species with different species occurring in different years as well as seasons (Sapphire McMullan-Fisher, pers. comm.) Thus the single sampling for fungi in this study did not necessarily provide a representative measure of fungal beta diversity from which comparisons with other taxa could be made.

When beta diversity of the whole study area (1.3 km^2) was considered, regardless of forest types contained within it, vascular plants had the lowest diversity (7.43) , followed by fungi with a beta diversity of 14.65. The turnover of beetles and spiders was higher than for plants with a beta diversity of 24.45 for beetles and 29.04 for adult spiders.

4.8.1.2 Regional variation

At the regional scale beta diversity indices were calculated for each forest type within

each region as well as for each region regardless of forest type (Table 3.11).

	SPECIES	Spp Rich	β–diversity indices REGION						β–*	REGION		
			Hobart		Levendale		Swansea			Hob	Lev.	Swa.
			DOB	DPU	DOB	DPU	DOB	DPU				
Modified Whittaker's Index	Beetles	186	29.52	26.57	21.56	18.98	32.11	27.97	18.98	40.00	36.04	35.18
	Spiders (all)	196	29.47	25.45	29.47	15.56	31.11	20.74	15.56	38.43	28.03	29.29
	Spiders (adults)	182	34.67	30.59	28.89	16.77	32.50	22.61	16.77	41.71	30.21	30.85

Table 3.11 Table of Whittaker's B-diversity index modified by Harrison *et al*, (1992), for the regional species. Sampling occurred in November. (*= for all three regions combined).

Within each region beta diversity was higher in DOB forest type than DPU. This was the opposite of the trend for Mt Wellington, however the Mt Wellington samples contained species present in April and February and November whereas regional scale sampling only occurred in November.

Overall beta diversity of each region was similar for beetles and spiders, with the index ranging from 16 to 19.

4.8.1 Do assemblages of beetles and spiders correspond to mapped forest types?

4.8.1 Non-parametric MANOVA

Non-parametric MANOVA (NP-MANOVA) was used to analyse species occurrence across sites in the foothills of Mt Wellington. It provided a test for whether species from the same forest type group were more similar than species from other forest type groups. The output below is from a one-way ANOVA design consisting of sites (samples) grouped within 6 different forest types (factors) with 4 replicates of each. Data were fourth root transformed and distances between pairs of samples were calculated using the Bray-Curtis dissimilarity measure which is appropriate for zero-inflated data. Results are based on 4999 permutations. Pair-wise *a posteriori* tests

were performed on the six forest types.

Non-parametric Multivariate Analysis of Variance

Variables	Source	df	SS	MS	F	P
Beetles	Forest	5	23696.8750	4739.3750	2.1242	0.0002
152 spp	Residual	18	40160.2199	2231.1233		
	Total	23	63857.0949			
Spiders	Forest	5	24452.3260	4890.4652	2.0497	0.0002
(adults)	Residual	18	42947.6129	2385.9785		
187 spp	Total	23	67399.9390			

Table 3.12 Results of one-way anovas for species occurrences in different forest types.

NP MANOVA Tests among groups in factor 'forest'

Beetles			Spiders (adults)		
Groups	t	P	Groups	t	P
(WRE, WOB)	1.1165	0.2298	**(WRE, WOB)**	1.4635	**0.0294**
(WRE, DOB)	1.349	**0.0308**	(WRE, DOB)	1.2724	0.0564
(WRE, DTO)	2.0596	**0.0292**	**(WRE, DTO)**	1.8556	**0.0292**
(WRE, DPU)	1.4294	**0.0282**	**(WRE, DPU)**	1.5386	**0.0282**
(WRE, DAM)	2.1843	**0.0316**	**(WRE, DAM)**	2.0254	**0.0316**
(WOB, DOB)	1.1824	0.115	**(WOB, DOB)**	1.3061	**0.0262**
(WOB, DTO)	1.8658	**0.0298**	**(WOB, DTO)**	1.6534	**0.0298**
(WOB, DPU)	1.1474	0.2128	**(WOB, DPU)**	1.4408	**0.0302**
(WOB,DAM)	1.8976	**0.0276**	**(WOB, DAM)**	1.7384	**0.0276**
(DOB, DTO)	1.4201	**0.0262**	(DOB, DTO)	1.1224	0.1462
(DOB, DPU)	1.0121	0.4938	(DOB, DPU)	1.0273	0.3878
(DOB, DAM)	1.5742	**0.0316**	(DOB, DAM)	1.1082	0.2612
(DTO, DPU)	1.0649	0.2816	(DTO, DPU)	1.2435	0.0824
(DTO, DAM)	1.1034	0.1882	(DTO, DAM)	0.9892	0.5432
(DPU, DAM)	1.1544	0.253	(DPU, DAM)	1.4062	0.057

Table 3.13 Pairwise *a posteriori* comparisons of dissimilarity in assemblages between groups of forest type. Significant pairwise differences between forest types appear in bold type (at $p < 0.05$ level of significance).

Examination of NP-MANOVA results for beetles (Table 3.12) indicates that overall

there was a significant difference in occurrence of beetles in different forest types (p=0.0002). However, pair-wise *a posteriori* comparisons of forest types (Table 3.13) indicates that the differences in occurrence were not significant for all forest types.

Beetle assemblages in wet WRE were significantly dissimilar to beetle assemblages in all dry forest types ($p < 0.032$). Beetle assemblages in DTO were not significantly different to DAM, and assemblages in WOB were not significantly different to those in DOB. Beetle assemblages in the wet and dry *E. obliqua* forest sites (WOB and DOB) were, however, significantly different to DAM ($p= 0.0276$ and $p= 0.0316$ respectively) and DTO ($p= 0.0298$ and $p= 0.0262$ respectively).

For spiders there was a consistent dissimilarity in spider assemblages in wetter forest types compared to those in drier forest types. WOB was dissimilar to all other forest types including the other wet type, WRE, suggesting that factors other than moisture might be relevant. WRE was significantly dissimilar to all other forest types except DOB which was nearly significantly different ($p = 0.0564$). Where there was an insignificant difference between pairs of forest types then species distribution may be a response to factors other than forest type or due to high variation.

Dispersion of the spider and beetle data was tested before the significant of the NP-MANOVA could be interpreted as showing that invertebrates from the same forest type were more similar than assemblages from different sites. Dispersion was different in each case (Figure 3.14).

Variables	Source	df	SS	MS	F	P
Beetles	Forest	5	517.494	103.4989	3.5514	0.0244
152 spp	Residual	18	524.5789	29.1433		
	Total	23	1042.0734			
Spiders	Forest	5	126.6726	25.3345	0.8502	0.5271
(adults)	Residual	18	536.3523	29.7973		
190 spp	Total	23	663.0249			

Table 3.14 Permutational Test of Multivariate Dispersion: tests for heterogeneity in the average dissimilarities of points from the central location of their group.

There were no significant differences in the multivariate dispersion of adult spiders among groups of forest type (p= 0.5271) and, therefore, pairwise *a posteriori* comparisons among forest types were not conducted for spiders. Non-significant multivariate dispersion indicates that the dispersal of spider data at sites within the same forest forest type was as variable as that among forest types.

Multivariate dispersion of the beetle data was, however, significant (p= 0.0244), indicating that while NP-MANOVA derived significant effects of forest type on beetle data, that a significant amount of variation existed in the multivariate dispersion of beetles between groups. Forest type DTO, in particular, seemed to be central to a lot of the calculated dispersion of beetle data, (Table 3.14), suggesting that beetles assemblages in sites classified as DTO are highly variable.

Results of *a posteriori* pairwise tests among groups in factor 'forest' appear in Table 3.15.

	Beetles			
Groups	t	P	Poss #perm	Groups
(1, 2)	1.2912	0.2574	35	(1, 2)
(1, 3)	1.1315	0.3132	35	(1, 3)
(1, 4)	2.3964	0.0872	35	(1, 4)
(1, 5)	3.0762	**0.0316**	35	(1, 5)
(1, 6)	0.9207	0.3986	35	(1, 6)
(2, 3)	0.4869	0.6	35	(2, 3)
(2, 4)	2.6758	**0.0298**	35	(2, 4)
(2, 5)	0.3864	0.6824	35	(2, 5)
(2, 6)	1.7177	0.1428	35	(2, 6)
(3, 4)	3.3596	**0.0294**	35	(3, 4)
(3, 5)	1.4113	0.286	35	(3, 5)
(3, 6)	1.5918	0.1952	35	(3, 6)
(4, 5)	7.0445	**0.0322**	35	(4, 5)
(4, 6)	0.2376	0.9162	35	(4, 6)
(5, 6)	2.5944	0.115	35	(5, 6)

Table 3.15 Pair-wise *a posteriori* comparisons of beetle assemblages among forest types.

	Average within-group dissimilarities	
Beetles	WRE	64.090
	WOB	73.290
	DOB	69.475
	DTE	55.635
	DPU	75.537
	DAM	57.425
Spiders (adult)	WRE	60.581
	WOB	71.107
	DOB	72.161
	DTE	70.081
	DPU	67.817
	DAM	69.404

Table 3.16 Average within group dissimilarity for beetles and spiders

	Average dissimilarities within/between groups					
Beetles	1	2	3	4	5	6
	1 64.090					
	2 70.876	73.290				
	3 73.219	75.043	69.475			
	4 80.845	83.007	70.235	55.635		
	5 78.784	77.163	72.792	67.057	75.537	
	6 85.643	85.209	74.847	58.169	69.463	57.425
Spiders (adult)	1	2	3	4	5	6
	1 60.581					
	2 74.485	71.107				
	3 71.601	77.357	72.161			
	4 83.317	84.524	73.752	70.081		
	5 74.492	78.169	70.842	73.913	67.817	
	6 87.206	86.407	73.100	69.768	77.025	69.404

Table 3.17 Matrices of Bray-Curtis dissimilarities within and between groups.

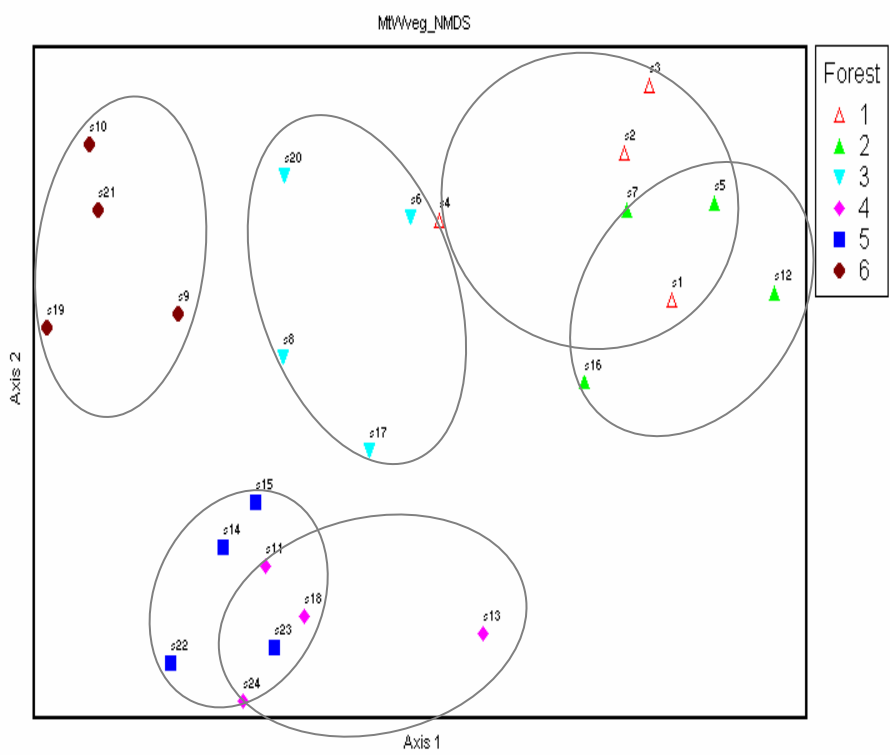
Matrices of Bray-Curtis dissimilarity indices within and between groups, (Figure 3.17), indicate that the dissimilarity between assemblages of species at sites with the same forest type (the diagonal of each matrix) are almost as high as the dissimilarity between assemblages in different forest types. This trend is more pronounced for the

spider assemblages.

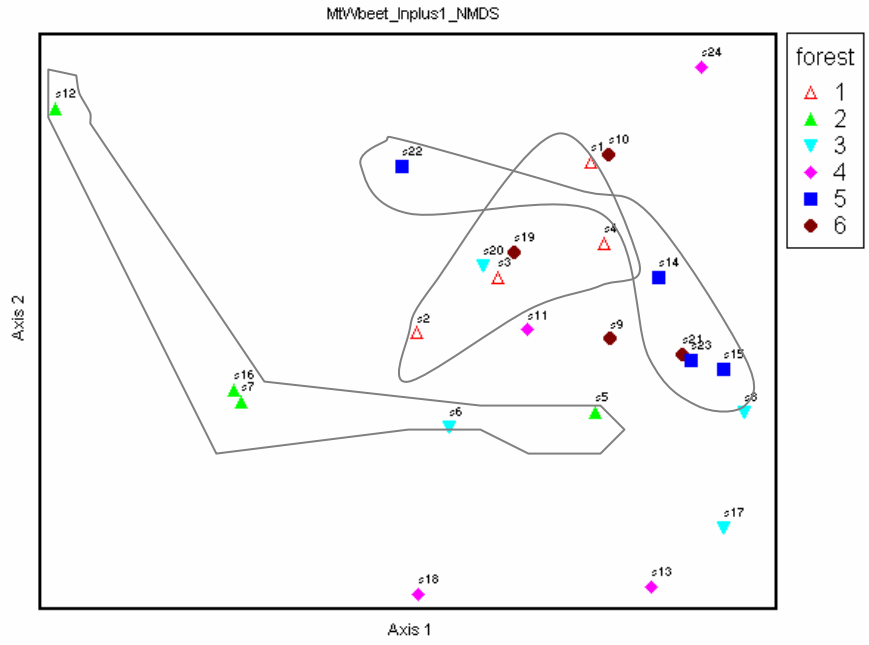
MDS ordinations of sites in beetle and in spider species 'spaces' provide a visual representation of the dissimilarity in assemblages between sites just discussed (Figure 3.21).

Since grouping sites by forest type did not provide a clear correspondence to species assemblages, the variation in species among the sites within each forest type was examined more closely.

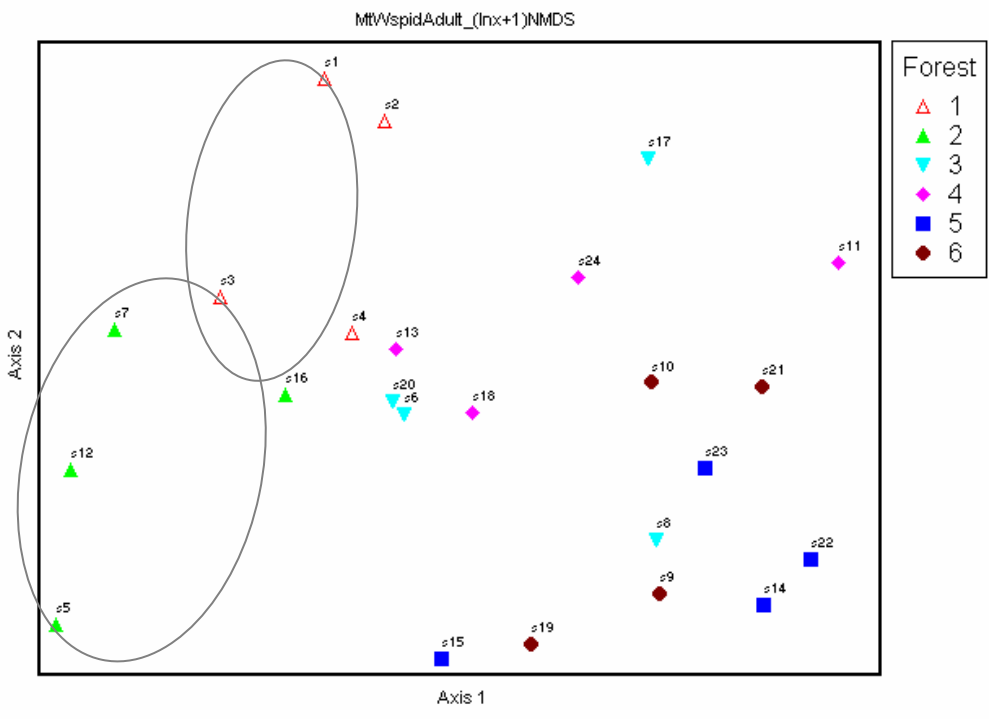
Nonmetric Multidimensional Scaling (NMDS) was appropriate for species data that is not necessarily normally distributed. Separate ordinations of matrices of beetle, spider (all), spider (adults), fungi, and vegetation species for each site provided a visual presentation of Bray-Curtis dissimilarity indices between assemblages at each site. Abundance data were transformed for beetle and spider abundances to ln(x+1) so that highly abundant species did not dominate the ordination patterns. Fungi volume and scored vegetation cover data were not transformed.



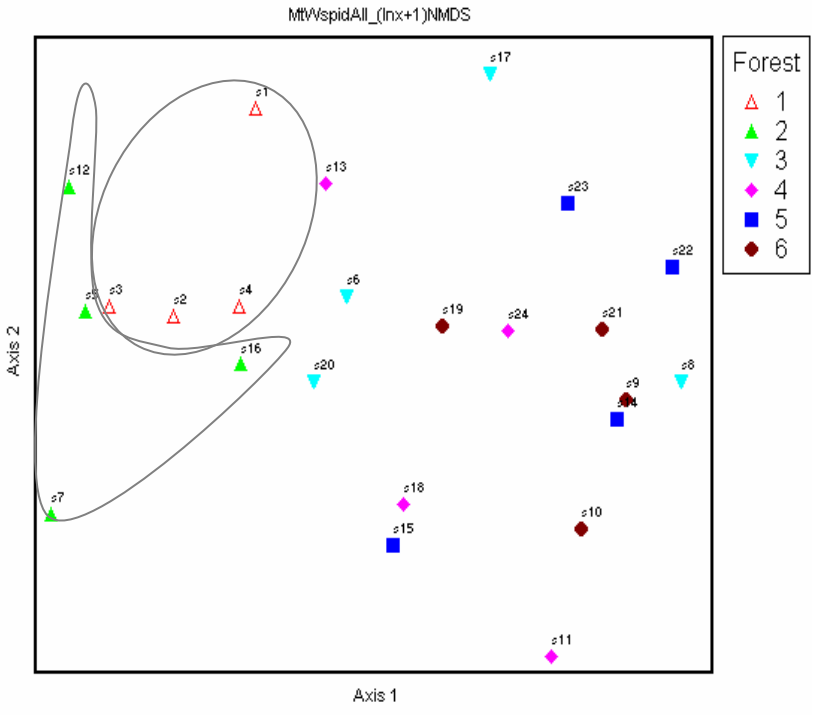
(a)Vegetation ordination: 2-D Stress = 9.1766, 400 iterations



(b) Beetle ordination: 3-D Stress = 11.30037, 63 iterations



(c) Adult spiders ordination: 2-D Stress =16.7265, 67 iterations



(d) All spiders ordination: 3-D Stress =12.48527, 48 iterations

Figure 0.21 Ordinations of sites in different species spaces. Sites grouped closer together share more similar species than those spaced further apart. Key to forest types: 1 = WRE, 2= WOB, 3= DOB, 4 = DAM, 5 = DPU, 6 = DTO.

Sites with similar assemblages may be assessed from the ordinations in Figure 3.21

where sites with more similar assemblages are grouped closer together and those that are more dissimilar are spaced further apart.

The ordination of sites in plant species space results in some discrete grouping of sites that reflect forest type quite well, particularly DTO and DOB. The horizontal ordination axis shows a degree of mesic separation of sites, with wetter WRE and WOB to the right and drier types to the left. The two wetter forest type sites are intermingled in the ordination, suggesting overlap of species, and their loose clustering implies variation from site to site within the same forest type. Overlap of vegetation species at sites located in drier forest types DAM and DPU areindicated by clustering of these sites amongst each other. Less difference in vegetation between sites resulted in closer clustering of those sites, though site 13 (DPU) has different species to any others. The vertical ordination axis separates sites separated DTO and DPU sites from the rest, indicating a difference in vascular plant species in these two forest types compared with the other types. The stress of 9.17671 for the ordination of sites by vegetation species suggests that the result is a fairly reliable plot of sites in relation to their original ranked distances. In this case the plot suggests that forest type is largely indicated by patterns in distribution of vegetation species.

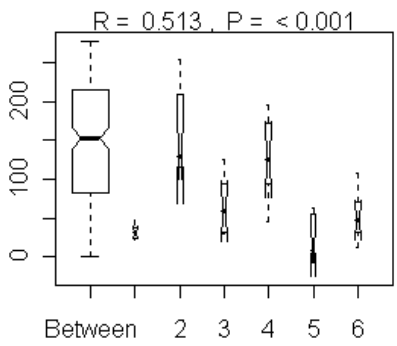
The ordination of sites in beetle and spider species spaces resulted in loose clustering of sites in similar forest type dominated by overlap between the forest types. Sites from quite different forest types were more closely clustered due to higher similarity in beetle species. This suggests that factors other than forest type may be influencing distribution of beetle and species. The ordination enables a preliminary investigation of spatial autocorrelation by referring to the map (Figure 2.1), where sites from different forest types that have clustered together due to similarity in beetle assemblages are not in adjacent patches. For example the pair of sites 21(DTO) and 23 (DAM) show a strong similarity in assemblages but are further separated by patches of DPU and DOB. Sites 3 (WRE), 19 (DTO) and 20 (WOB) have many species in common, despite other intervening forest types. In contrast, sites 8 and 20 are near each other in the same patch of DOB and are widely separated in the ordination due to few shared species. A more robust test for autocorrelation will be

conducted in a later section. The ordination 3-D stress value of 11.3 indicates that some caution should be exercised in interpreting this plot, and finer details should be disregarded as it cannot be reliably interpreted (McCune and Grace, 2002). However, the poor relationship between forest type and beetle assemblage is loosely demonstrated by the ordination.

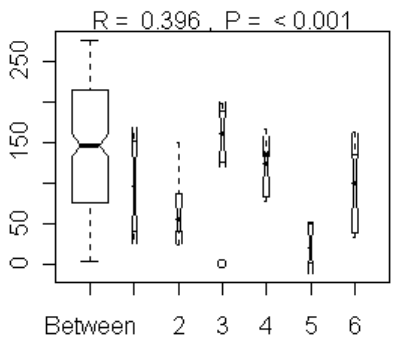
The horizontal axis separated mesic forest sites when ordinated by adult spiders and by all spiders but sites of the same forest type were still widely dispersed, suggesting that this factor alone was not enough to account for differences between sites. No pattern was discernable for separation of sites along the vertical axis. A stress of 16.7265 for the 2-D ordination of adult spiders and 12.4527 for a 3-D ordination of all spiders meant that there is some unreliability in the ordinations so caution should be exercised when interpreting them.

4.8.1 ANOSIM

A more rigorous test of these differences in assemblages grouped by forest type was pursued with an Analysis of Similarity (ANOSIM) which was suited to the one-way design of this study. The analysis, conducted in R, is a non-parametric permutation of dissimilarity ranks from a Bray-Curtis matrix of dissimilarity between pairs of sites to test for a significant difference in the composition of assemblages at different sites. The number of permutations was 10,000.



Beetle community similarity with forest type



Spider (all) community similarity with forest

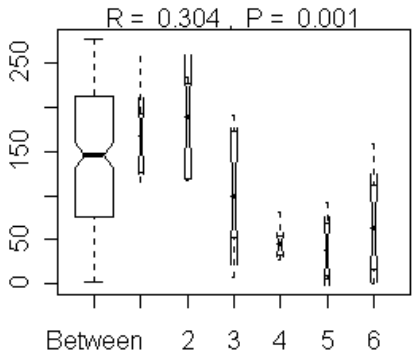
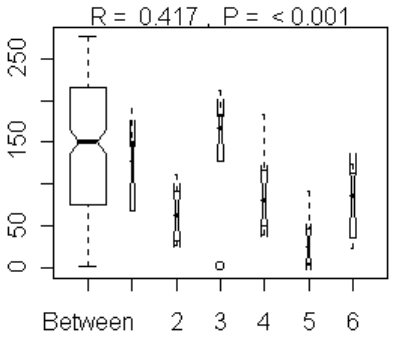
	type
	
Fungi community similarity with forest type	Spider (adult) community similarity with forest type
	Species R p beetles 0.513 <0.001 spiders (all) 0.3963 <0.001 Spiders (adults) 0.4166 <0.001 fungi 0.3037 <0.001 (Based on 1000 permutations)

Figure 3.22 The effect of forest type on species communities. Boxplots portray the mean ranks of dissimilarity between and within groups. Key to forest types: 1 = WRE, 2= WOB, 3= DOB, 4 = DAM, 5 = DPU, 6 = DTO.

For ANOSIM (Figure 3.22) the R statistic has a range of 1 to -1 with a value of zero if groups are independent and was significant for all analyses ($p < 0.001$). Analysis conducted for similarity of beetle assemblages with forest type showed the strongest difference in beetle species among different mapped forest types ($R = 0.513$). The difference for adult spiders alone ($R = 0.41166$) was stronger than when all spiders were analysed ($R = 0.3963$). Fungi data showed weakest differences between forest types ($R = 0.3037$).

The boxplot of beetles shows little variation in beetle species at different sites within forest type WRE, while there is wide variation between species at different sites within the same forest type for all other forest types. Adult and all spider species

varied widely in sites within the same forest type for all forest types, which implies there was a lower relationship between forest type and spider species.

4.8.1 Do all forest types contribute equally to species variation?

Having investigated whether forest type has an effect on assemblages, a CAP analysis was able to reveal the amount of variation explained by forest type and which forest types explained any of that variation.

CAP analysis using discriminant analysis to test for differences among forest types (groups) in beetles and spiders (adults and juveniles; and adults only) provided the results in Table 3.18. Cross validation of the canonical correlations using a leave-one-out permutation test are included. All analyses used fourth root transformed species data and Bray-Curtis dissimilarity indices.

Effect of Forest type on:	m	Variation explained (%)	Successful Allocation to Forest Type (%) WRE	WOB	DOB	DTO	DPU	DAM	Total		p
beetles	7	71.435	50	75	25	50	0	75	45.833	0.069088	0.8558
Spiders (all)	7	64.498	100	75	75	25	0	0	45.833	0.909598	**0.0011**
Spiders (adults)	15	92.203	75	75	0	50	50	75	54.167	0.385911	0.3944

Table 3.18 Summary CAP results to determine the effect of forest type on beetle and spider assemblages at each site. 'm' is the number of first principal coordinates selected by the program during the analysis. 'Variation explained' refers to the variation explained by the first m principal coordinates.

Successful classification of beetles to forest type was highest (75%) for forest types

WOB and DAM, while there was zero successful allocation to DPU. Assemblages of beetles in DOB (25% successful allocation) were highly random, and even more random in DPU but more discrete and distinctive in forest types WOB and DAM. CAP analysis indicated that forest type was not significant for beetles, with a very low squared canonical correlation (δ^2) of 0.069088 (p= 0.8558).

For all spiders leave-one-out allocation was 100% successful in allocation to forest type 1 (WRE) but had zero success with forest types DPU and DAM. CAP analysis indicated that forest type was highly significant for all spiders, with δ^2 = 0.909598 (p= 0.0011).

When juvenile spiders were removed from the analysis, allocation was more consistently successful across each of the forest types apart from total failure to successfully allocate adult spiders to forest type DOB (0%). The CAP analysis produced a lower squared canonical correlation (δ^2 = 0.385911) than when all spiders were included, and its value was no longer significant (p= 0.3944) ie forest type was not significant for adult spiders alone.

CAP output of correlations of canonical axes with original axes generated low correlations. Examination of the correlations enabled the species more highly correlated with the canonical axes to be identified. Species most highly correlated with canonical axes, with a correlation value > 0.6, are listed in Table 3.19. They are the species contributing most to multivariate distribution of beetles among forest types.

		Correlation value				
Assemblage	Species	Canonical axis				
		1	2	3	4	5
Beetles	*Nemadini* sp.: Leiodidae		-0.6496			
	Thalycrodes australis: Nitidulae			-0.7076		
	Acrotrichis sp. : Ptilidae			0.6550		
	Scaphisoma sp. : Staphylinidae		-0.6017			
	Isopteron obscurum: Tenebrionidae				0.6621	
	Tetrabothrus claviger: Staphylinidae				0.6381	
Spiders (all)	*Suppuna picta*: Corrinidae	0.7654				
	Gnaphosidae NM34: Gnaphosidae				0.7757	
	Lycosidae NM1: Lycosidae				0.6321	
	Micropholcommatidae NM8: Microphol.	0.6129				
	Zodariidae NM26: Zodariidae	0.6372				
	Zoridae NM1: Zoridae	0.6176				
Spiders (adults)	*Hestimodema* A: Zoridae				0.7248	
Fungi	*Descolea sp* Bolbitaceae					0.8685
	Clavaria miniata complex: Clavariaceae					-0.6303
	Geastrum sp. B: Geastraceae					-0.8733
	Russula sp. pink: Russulaceae	-0.714				
	Stereum sp. C yellow: Stearaceae				0.6297	
	Leucopaxillus sp.: Tricholomataceae			0.685		

Table 3.19 Highest values for correlation of canonical axes with original axes from CAP analyses for forest type

The low correlation of most species with the canonical axes is demonstrated by the plot below where beetle species variation does not correspond to locations of sites (Figure 3.23).

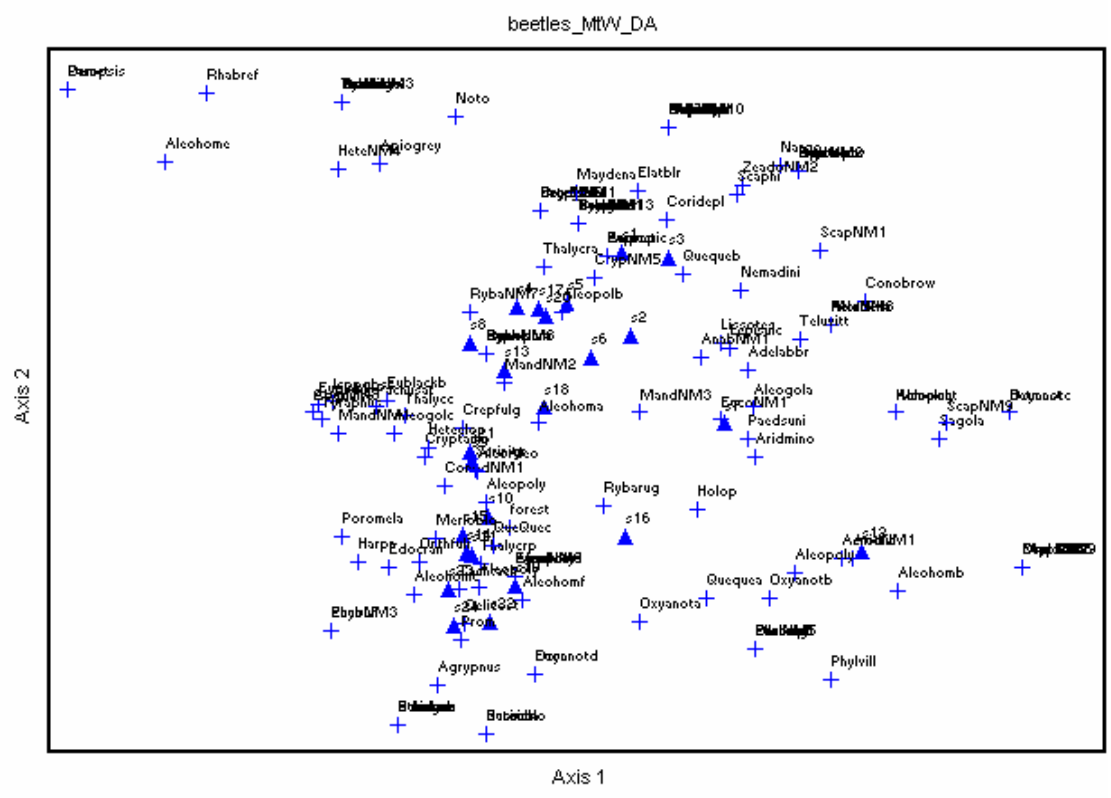


Figure 3.23 Canonical correlation of beetle species data plotted for the first two canonical axes. Crosses indicate species distributions and triangles indicate sites.

4.8.5.1 CAP CCA

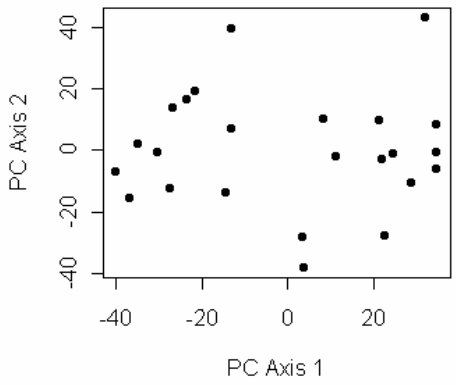
A slightly different canonical analysis of principal coordinates, this time under canonical correlation, provided an indication of the relationship between species distribution and environmental variables. In this analysis a slightly larger subgroup of beetles was found to be correlated with canonical axes, though most correlations were not really strong. The variables were independent of forest type:

The CAP (Anderson, 2004) analysis was by Canonical Correlation Analysis (CCA) enabling a multivariate eigenanalysis with a permutation test for the relationship between species distribution and environmental variables.

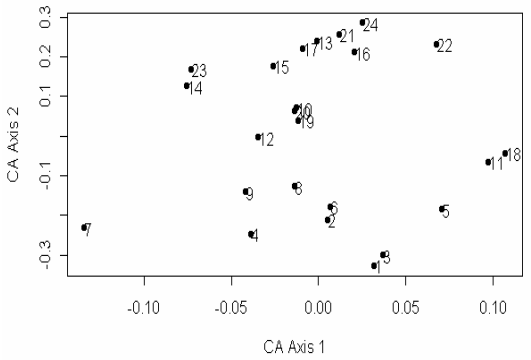
		Correlation value				
Assemblage	Species number and name	Canonical axis				
		1	2	3	4	5
Beetles	*Nemadini*: Leiodidae		0.7229			
	Zeadolopus NM2: Leiodidae		0.6476			
	Thalycrodes australe: Nitidulae					0.6944
	Thalycrodes cylindricum: Nitidulae	0.6858				
	Scaphisoma sp.: Leiodidae		0.7255			
	Rybaxis rugosus: Pselaphidae	0.6369				
	Mandalotus NM1: Curculiuonidae		-0.7734			
	Anotylus B: Staphylinidae				0.6102	
Spiders (all)	*Suppuna* NM1: Corrinidae				-0.8022	
	Gnaphosidae NM1: Gnaphosidae				-0.6715	
	Laetesia NM1: Linyphiidae				-0.6246	
	Mynogleninae NM33: Linyphiidae				0.6714	
	Storena flavipes: Zodariidae				-0.6545	
	Zodariidae NM12; Zodariidae				-0.6306	
Spiders (adults)	None					
Fungi	*Descolea* sp. Bolbitiaceae	-0.6839				
	Geastrum sp. B: Geastraceae		-0.7046			

Table 3.20 Highest values for correlation of canonical axes with original axes from CAP analyses for environmental variables.

The plots of principal component axes and canonical axes (Figure 3.34) represent the quite variable differences in composition and abundance of beetles species at each site based on environment variables. Similar variation occurred in the plots for spiders so they are not reproduced here.



Principal coordinates plot for beetles



Canonical plot for beetles

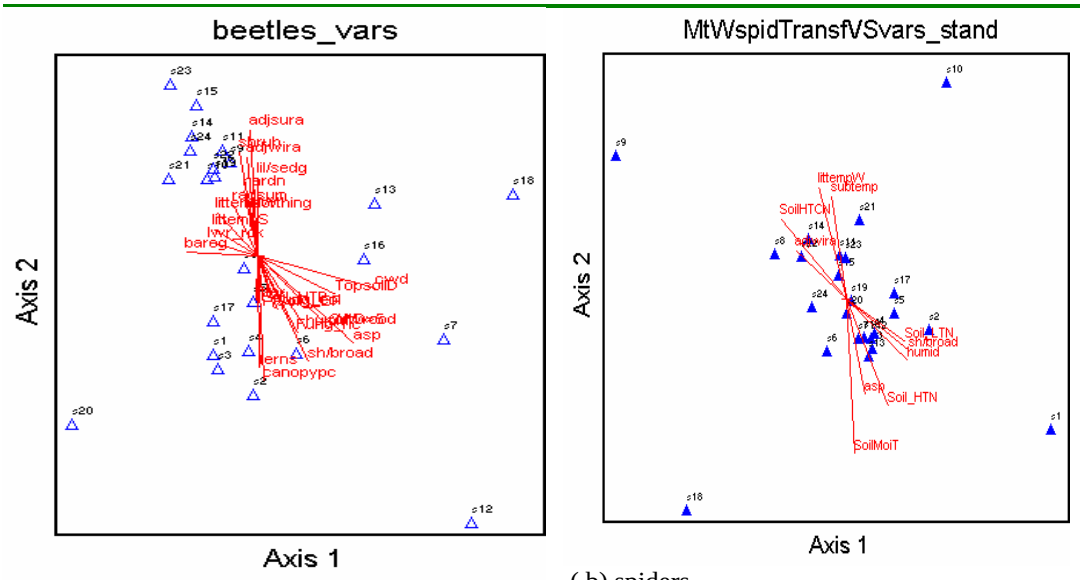
Figure 3.24 Plots of the first two principal coordinates axes and canonical axes from CAP analysis for beetles.

Having identified wide variation in assemblages among sites even within the same forest type, the next phase of the analysis was to identify the environmental variables that species of beetles and spiders were responding to other than mapped forest type.

4.8.1 Which environmental variables are related to species distributions?

4.8.6.1 NMDS

All environmental variables were included in NMDS ordinations of species data in which biplots of environmental data identified variables with the strongest relationship with species variation. This enabled the number of variables to be reduced, for further analyses, to those contributing most to variation in species distributions.



(a) beetles (b) spiders

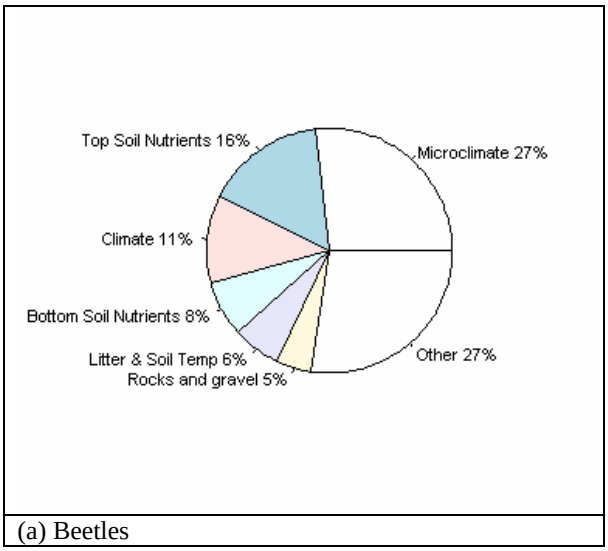
Figure 3.25 NMDS ordination of sites in species space with biplots of the variables contributing most to the ordination axes., cutoff: $r^2 = 0.2$

The clustering of sites in species space (Figure 3.25) corresponded to two quite distinct groups for both beetles and spiders. Variation in beetle assemblages caused vertical separation of sites along a moisture/temperature gradient (Axis 2). Thus beetles at sites in wetter forest types were associated with higher canopy cover, ferns, broad leaf shrubs and higher volume of fungi. At the drier end of the gradient beetles from drier DPU, DAM and DTO were associated with higher summer and winter radiation and higher litter temp. A further separation of sites along Axis 1 related to the structure of ground cover, with beetles from wetter sites more closely associated with greater volume of coarse woody debris, greater depth of the top soil and higher levels of phosphorus in the top soil (A horizon). The other end of the groundcover gradient was characterised by the amount of rock in the subsoil (B horizon), shrub cover of the ground, soil hardness and area of bare ground.

Fewer environmental variables explained the distribution of adult spiders. Axis 2 represented a moisture gradient that separated spiders associated with higher humidity at ground level, higher soil moisture and broad leaf shrubs, from higher radiation at

ground level after allowing for canopy cover, higher subsoil temperatures in winter and higher litter temperature in winter. Axis 1 separated the sites along a gradient of soil nutrients, with spiders in the wetter sites associated with higher levels of nitrogen in the top soil (A horizon) and higher minimum levels of nitrogen in the subsoil (B horizon). Spiders in the drier sites were associated on the soil nutrient gradient with a higher carbon to nitrogen ratio in the topsoil (A horizon).

For beetles the above results are supported by the variation explained by the principal coordinates axes resulting from the Cap (CCA) analysis which are presented as a piechart, Figure 3.26.



(a) Beetles

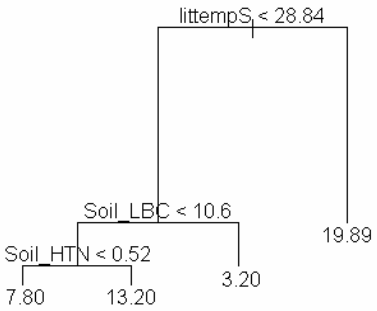
Figure 3.26 Variation of beetle data explained by Principal coordinates axes from canonical correlation analysis with environmental data.

4.8.6.2 Regression tree models

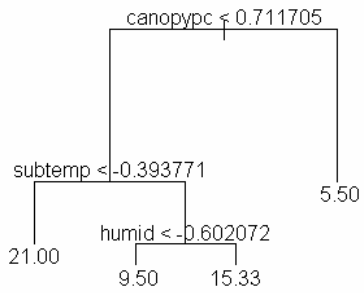
Regression tree models were built in R using the tree package (Ripley, 2007) to determine which of the numerous environmental variables measured were important to beetle and spider distribution. Rarer species (abundance less than 5) were removed from the data (as indicated under each tree) since their occurrence was not significant enough to detect patterns with environmental variables. All environmental variables were used.

In the output diagrams (Figure 3.27) the improvement in prediction error obtained by the split is proportional to the depth of the tree below each split. At each node the variable that distinguishes best between observations is identified along with the value at which the split occurs. The leaves of the tree present the mean of species present in that particular split of the data.

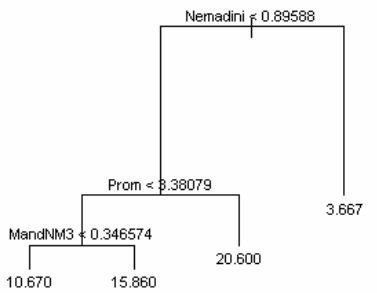
The first set of regression trees below regress site against different multivariate variables: environmental, beetle abundance, spider abundance and fungi volume.



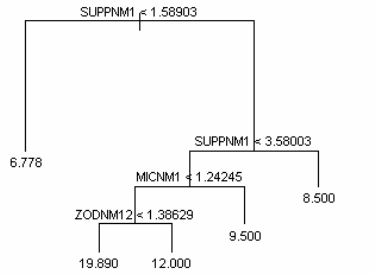
(a) Site against environmental variables cut = 3



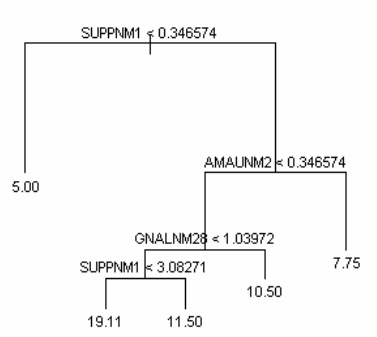
(b) Site against standardised environmental variables cut = 6



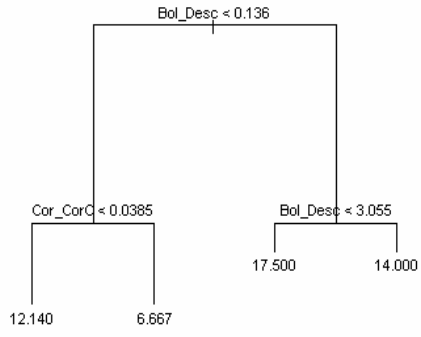
(c) Site against Beetles



(d) Site against Spiders(all)



(e) Site against Spiders (adults)



(f) Site against Fungi

Figure 3.27 Regression trees for site regressed against environmental variables with two different grouping levels (a) cut = 3, and (b) cut = 6, and site against (c) beetles, (d) spiders (all), (e) spiders (adults), and (f) fungi.

Regression trees in Figure 3.27 indicated that three variables were valuable predictors of site difference. At a finer scale (cut =3) (Figure 3.27 a) the variables were litter temperature, the minimum values of bottom soil carbon content (Soil LBC), and the highest values of nitrogen in the top soil (Soil HTN). These variables only applied to a small number of the 24 sites. Most (mean 19.4) had a higher litter temperature > 28.84). For this reason the analysis was repeated with a cut of 6 (Figure 3.27 b). This produced a grouping of the sites based on canopy cover less than 71% which corresponded to low subsoil temperatures at a mean of 21 of the sites and low humidity at a mean of 9.5 of the sites. Generally there was a predictable variation in sites in relation to environmental variables such that canopy cover (< 0.711705) corresponded to low subsoil temperature at a mean of 21 sites, but higher subsoil temperatures corresponded to differences in humidity at sites.

A predictable variation in the sites was also discernable such that the abundance of *Nemadin*i sp. (<0.9) corresponded to high abundance of *Promecoderus* sp. at a mean of 21 sites, and low numbers of *Promecoderus* sp. (< 3.38) corresponded to differences in abundances of *Mandalotus* NM3 at different sites.

The abundance of the spider species *Suppuna* NM1 provided predictable variation in sites in relation to spiders. The variation was slightly different for adults only and adult plus juvenile assemblages. For all spiders (Figure 3.27d) an abundance of *Suppuna* NM1 < 1.6 occurred at a mean of 6.8 sites. *Suppuna* NM1 abundance greater than 1.6 in fact corresponded to its higher abundance (>3.58) at a mean of 8.5 sites. Between these two values its abundance corresponded to higher abundance of Micropholcommatidae NM1 (>1.2) at an average of 9.5 sites. Lower abundances of Micropholcommatidae corresponded to that of Zodariidae NM12.

With the exclusion of juvenile spiders (Figure 3.27e), the predictable variation in sites was that higher *Suppuna* NM1 abundandance (> 0.35) corresponded to a higher

Amaurobiidae NM2 abundance at an average of 7.75 sites. Lower Amaurobiidae abundance (< 0.34) corresponded to higher Gnaphosidae NM28 abundance at a mean of 10.5 sites. Lower Gnaphosiidae NM28 abundance (<1.03) corresponded to a *Supunna* NM1 abundance > 3 at a mean of 11.5 sites.

For fungi it was predictable that the occurrence of lower volumes of *Descolea* spp. across the sites (<0.14) corresponded to occurrence of *Cortinaria* C, while *Descolea* spp. volumes greater than this further differentiated sites. A volume of *Descolea* spp. greater than 3.06 occurred at a mean of 14 sites and a volume between 14 and 3.05 occurred with greater frequency at a mean of 17.5 sites.

4.8.6.3 BIOENV

The Bioenv function sequentially adds a variable to the model and rejects it if that combination of variables does not improve the fit of the model to the data set. To ensure that the order in which variables are added did not affect the outcome, the function was run several times on a dataset with the order of the variables randomly shuffled manually. In each case the same optimal subsets were selected by the program.

	Best Subset of measured environmental variables (out of 56 variables)	Spearman correlation	Best subset of plant species variables (out of 147 spp.)	Spearman correlation
Beetles	Forest type Canopy cover Shrub cover Coarse woody debris cover Humidity ground level Rotting wood volume	0.674014	*Bedfordia salicina* *Coprosma quadrifida* *Eucalyptus obliqua* *Gonocarpus tetragynus* *Geranium sp.* *Pimelea humilis* *Pomaderris apetala* *Tetratheca labillardierei*	0.7137126
Spiders (all)	Forest type Canopy cover Litter depth Humidity ground level	0.597528	*Austrodanthonia* sp. *Bedfordia salicina* *Billardiera longiflora* *Coprosma quadrifida* *Gonocarpus tetragynus*	0.5754979
Spiders (adult)	Forest type Canopy cover Shrub cover Litter depth Humidity ground level Soil hardness Rotting wood volume	0.6539672	*Bedfordia salicina* *Billardiera longiflora* *Coprosma quadrifida* *Gonocarpus tetragynus*	0.6359896

Table 3.21 Subsets of environmental variables and vegetation species that shared the nearest dissimilarity rank correlation with species dissimilarity ranks.

The subsets of variables that had the closest dissimilarity ranking to those of the multivariate species data were quite small. Variation in beetle assemblages was most closely correlated with six environmental variables (forest type, canopy cover, shrub cover, coarse woody debris cover, humidity at ground level and volume of rotting wood, correlation 0.674014). One tree species (*Eucalyptus obliqua*), three shrub species (*Bedfordia salicina, Pomaderris apetala* and *Coprosma quadrifida*), several small plants to low bushes (*Geranium* sp., *Pimelea humilis*, and *Tetratheca labillardierei*) as well as a perennial herb (*Gonocarpus tetragynus*) were most closely correlated with variation in beetle assemblages (correlation 0.7137126).

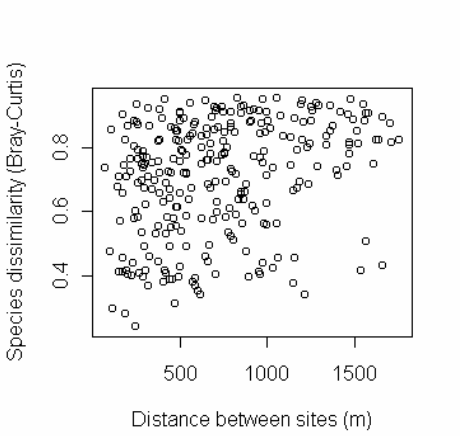
A similar but smaller subset of environmental variables showed highest correlation with all spiders. As for beetles, forest type, canopy cover and humidity at ground level were highly correlated with all spider distributions. Litter depth was the other

significant variable in the subset which was less highly correlated (0.597528) than the subset for beetles. The optimal subset of correlated variables for adult spiders was slightly larger than that for all spiders, suggesting more specific environmental requirements. Forest type, canopy cover, shrub cover, humidity at ground level and rotting wood volume as well as litter depth and soil hardness are variables that were correlated with adult spiders assemblages (correlation 0.653672). Adult spiders were more highly correlated with almost the same set of plant species as all spiders: *Bedfordia salicina*, *Billardiera longiflora*, *Coprosma quadrifida*, and *Gonocarpus tetragynus* (correlation 0.6359896 for adult spiders). The addition of *Austrodanthonia* sp. completed the subset with the highest correlation for all spiders (0.5754979).

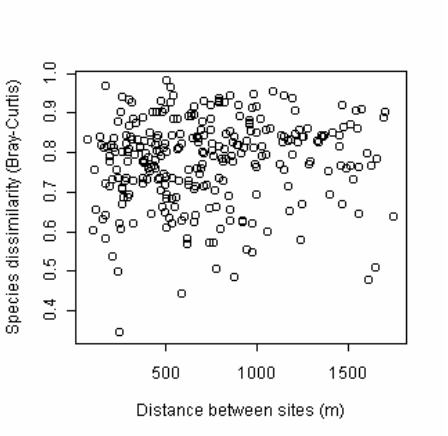
4.8.1 Accounting for spatial variation

4.8.7.1 MANTEL test

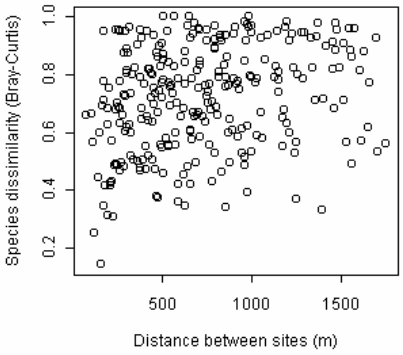
A Mantel style comparison of two distance matrices, species dissimilarity (Bray-Curtis) between pairs of sites and geographic distance (m) between pairs of sites produced a vector for each dissimilarity matrix which is plotted below to provide a visual indication of whether or not sites that are close together are more similar than those that are further apart.



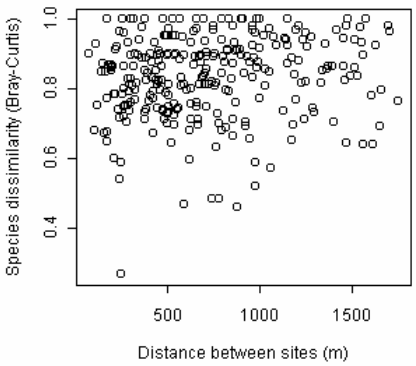
(a) Beetles Rho = 0.3066



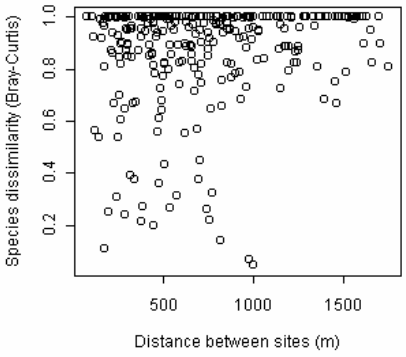
(b) Spiders (all) Rho = 0.1435



(c) Vegetation species Rho= 0.4126



(d) Spiders (adults) Rho = 0.1542



(e) Fungi Rho = 0.1536

Figure 3.28 Plots of distances between pairs of sites against species dissmilarity between pairs of sites (Bray-Curtis dissimilarity) for each of the matrices of species assemblages: beetles, spiders (all), spiders (adults only), fungi and vegetation. Spearman's Rank correlation coefficient (rho) appears below each plot.

The value of Spearman's Rank correlation coefficient (rho) for each pair of vectors is indicated for each plot, higher values being more significant. The rho values are generally low which indicates that the assemblages of species at sites that were geographically closer together were not more similar than those that were further apart.

4.8.7.2 Partitioning variation

Partitioning the species variation by explanatory matrices was conducted on Hellinger transformed data using RDA (in R) to account for variation due to environmental, spatial and plant species components and their interactions. Explanatory matrices consisted of the best subsets of variables selected by maximum rank correlation with dissimilarities of the species data using the exploratory Bioenv function in R.

The final set of ten environmental variables for beetles, after removal of correlated variables, was forest type, canopy cover, shrub cover at ground level, coarse woody debris, humidity at ground level, volume of rotting wood, sub soil moisture, total volume of fungi, top soil (A horizon) minimum carbon levels, and maximum top soil (A horizon) phosphorus levels. The final set of plant species was: *Acacia verniciflua*, *Austrodanthonia* spp, *Eucalyptus obliqua*, *Olearia viscosa*, *Pultenaea juniperina*.

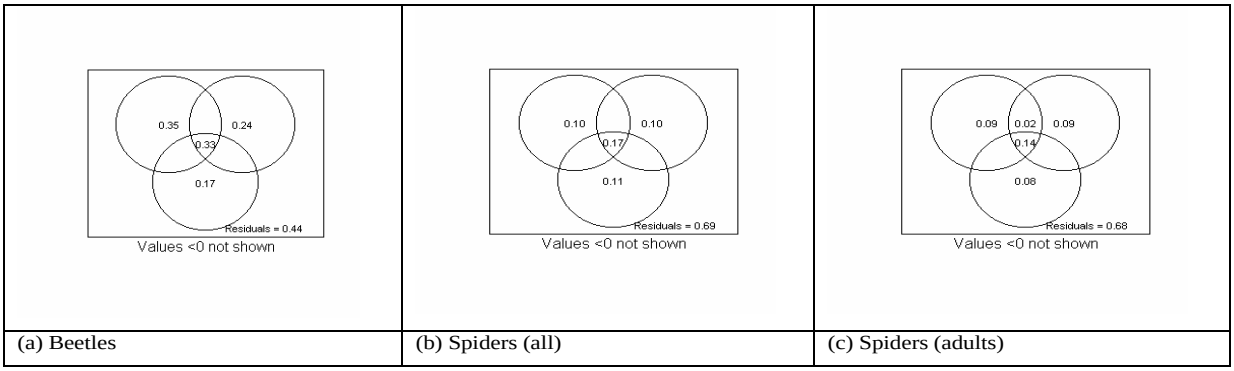
The final set of seven environmental variables for spiders, after removal of correlated variables, was forest type, canopy cover, shrub cover at ground level, humidity at ground level, soil hardness, litter temperature in summer and total volume of rotting wood. The final set of plant species was: *Austrodanthonia* spp, *Bedfordia salicina*, *Billardiera longiflora* and *Gonocarpus tetragynus.*

CCA was performed on the full set of variables, then successively partitioned. P

values were significant after 200 permutations of residuals under the reduced models.

	Total variation explained (SS)	Variation component	Degrees of freedom	R^2	Partial components	adjusted R^2
Beetles	10.273 (variance 0.44665)	E	10	0.59051	[a] E - SE-VE	0.35307
		S	5	0.40868	[b] S - SV-SE	0.24164
		V	6	0.38811	[c] V- SV -VE	0.16838
		E+S	15	0.78861	[d] E-S	-0.20622
		S+V	16	0.58656	[e] S-V	-0.12490
		E+V	11	0.79274	[f] V-E	-0.20323
		E+S+V	21	0.96179	[g]	0.33391
					[h]Unexplained (Residual)	0.43936
Spiders (all)	11.337 (variance 0.49291)	E	7	0.43094	[a] E - SE-VE	0.09547
		S	4	0.32821	[b] S - SV-SE	0.09915
		V	10	0.50495	[c] V- SV -VE	0.10942
		E+S	7	0.58517	[d] E-S	-0.00444
		S+V	11	0.79527	[e] S-V	-0.07622
		E+V	17	0.69434	[f] V-E	-0.07734
		E+S+V	14	0.94038	[g]	0.16829
			21		[h]Unexplained (Residual)	0.68567
Spiders (adult)	11.796 (variance 0.51288)	E	7	0.42825	[a] E - SE-VE	0.09426
		S	4	0.34899	[b] S - SV-SE	0.08629
		V	10	0.50122	[c] V- SV -VE	0.08342
		E+S	11	0.59965	[d] E-S	0.01798
		S+V	17	0.79908	[e] S-V	-0.03173
		E+V	14	0.69549	[f] V-E	-0.07354
		E+S+V	21	0.94053	[g]	0.13940
					[h]Unexplained (Residual)	0.68392

Table 3.22 Fractions of variation of Hellinger transformed beetle and spider data partitioned by three sets of explanatory variables: environmental (E), spatial (S) and plant species (V) matrices, with residual (unexplained) variation included.



(a) Beetles | (b) Spiders (all) | (c) Spiders (adults)

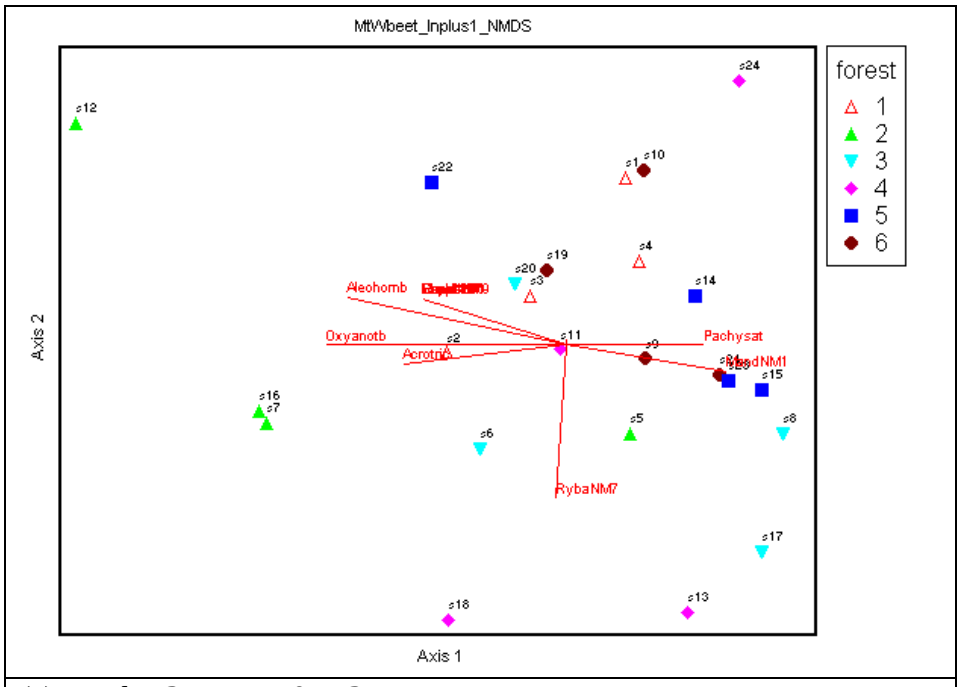
Figure 3.29 Diagrams of partitioned variation as fractions of species data variation. Circles represent the three explanatory matrices: Environmental (upper left circle), Spatial (upper right circle) and Vegetation species (lower central circle). The fraction of unexplained variation

appears as residuals.

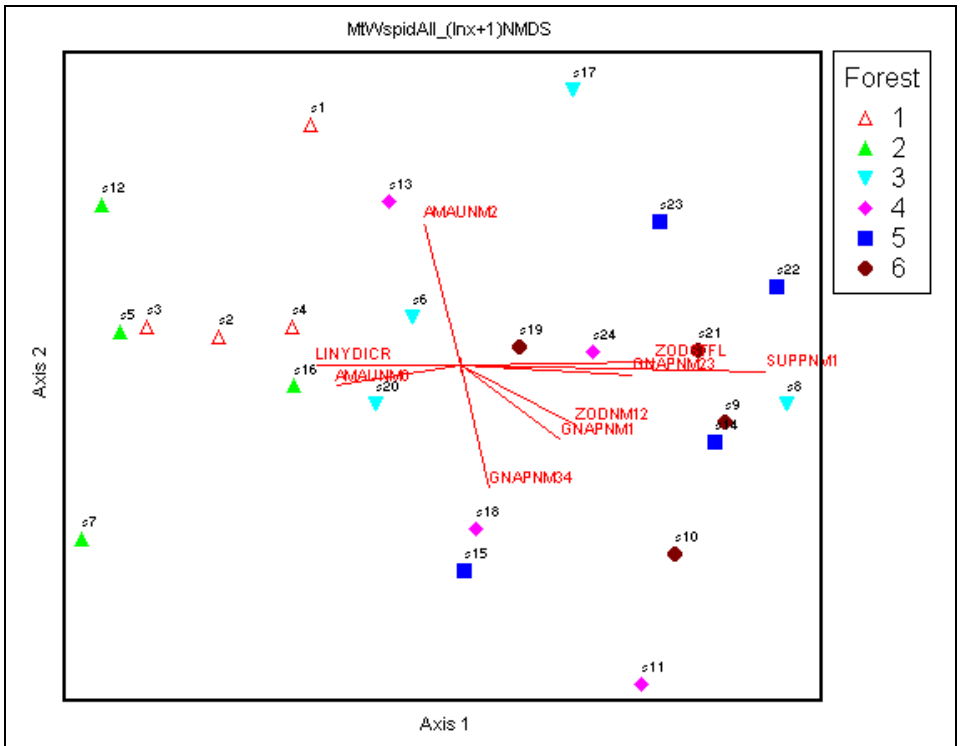
The largest amount of explainable beetle variation (Table 3.22 and Figure 3.29a) was explained by environmental variables (35%), while spatial variation explained 24% and plant species explained the least (17%) beetle variation. Less of the variation of spiders was explained by the three matrices which more or less equally explained about 10% for all spiders and less than 10% for adult spiders. Residuals were high in each case which indicated that unmeasured variables apart from spatial, plant species and measured environmental variables had not been examined.

4.8.1 Identifying Species that account for variation

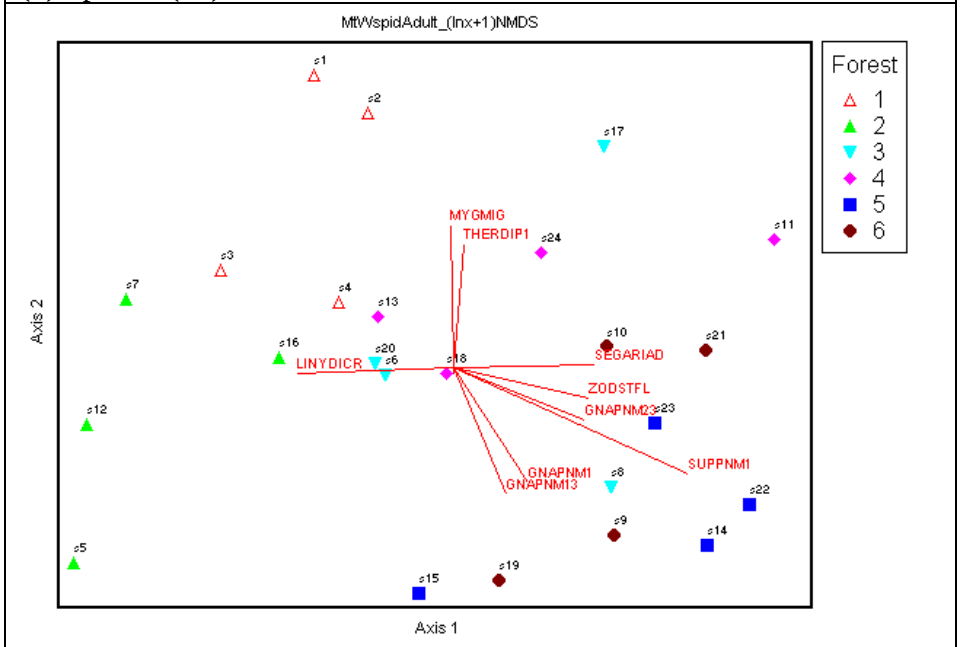
4.8.8.1 NMDS plus species biplots



(a) Beetles 3D stress 0.113



(b) Spiders (all) 3D stress 0.124



(c) Spider (adult) 3D stress 0.167

Figure 3.30 NMDS plots of sites grouped in species space with biplots of species contributing most to the clustering of sites indicated by the direction of the lines. Key to forest types: 1 = WRE, 2= WOB, 3= DOB, 4 = DAM, 5 = DPU, 6 = DTO.

The stress levels of the ordinations in Figure 3.30 were high so only tentative comments can be made about species whose variation in distribution contribute more

highly to ordination of sites in species space.

The wetter WRE and WOB sites were separated along the horizontal axis by beetle species that are mainly saprophages (*Anotylus* sp. B: Oxytellinae: Staphylinidae) and fungivores (*Acrotrichis* sp.: Ptilidae and *Thalycrodes australis* (Germar, 1848): Nitidulae along with a tiny (2mm) predator of these species (*Homalotus* sp B: Aleocharinae: Staphylinidae) (Figure 3.30a). At the other end of the axis were xylophagous weevils (*Pachyporopterus satyrus* (Pascoe, 1872): Curculionidae and *Mandalotus* NM1: Curculionidae) which separated some of the drier DTO and DAM sites. The tiny predatory Pselaphid species, *Rybaxis* NM7: Pselaphidae, separated some sites along the vertical ordination axis. No clear patterns related to forest type were discernable.

A separation of wet sites along the horizontal axis was discernable for all spiders (Figure 3.30 b) and adult spiders (Figure 3.30 c) with the web builders *Diplocephalus cristatus* (Blackwall, 1833): Linyphiidae and Amaurobiidae NM6: Amaurobiidae separating some of the wetter sites. Drier sites were separated by vagrant hunters (*Storena flavipedes* (Urquhart, 1893): Zodariidae, Gnaphosidae NM23: Gnaphosidae and *Suppuna* NM1: Corrinidae). Vertically the sites were most strongly separated for all spiders by the medium sized (15 mm) web builder Aaurobiidae NM2: Amaurobiidae at one end of the axis, and the medium sized vagrant hunter Gnaphosidae NM34: Gnaphosidae. A vertical separation of sites by adult spiders was due to a mygalomorph spider (*Migidae* sp: Migidae) and web builder, *Diplocephalus* sp. 1: Theridiidae, at one end of the axis and vagrant hunters at the other (Gnaphosidae NM1: Gnaphosidae and Gnaphosidae NM13: Gnaphosidae).

4.8.8.2 Indicator species analysis

Indicator species analysis (Dufrene and Legendre, 1977) of abundance and occurrence of a species in one group compared with all groups (McCune and Grace) was

performed in R with a Monte Carlo random reshuffling test of significance for 1000 permutations.

Species code			FOREST TYPE						Observed IV	IV From randomised groups		
	Avg	Max	WRE	WOB	DOB	DTO	DPU	DAM		Mean	S. Dev	p
Nargo	8	50	50	0	0	0	0	0	50	24.5	9.68	0.126
ZeadoNM2	**13**	**75**	**75**	**0**	**0**	**0**	**0**	**0**	**75**	**22.1**	**11.96**	**0.014**
Galerby	4	25	25	0	0	0	0	0	25	25	0.79	1
Agrypnus	8	38	0	0	0	13	38	0	37.5	24.6	13.02	0.355
Noto	8	50	50	0	0	0	0	0	50	23	10.74	0.137
Seringra	4	25	0	0	0	0	25	0	25	25	0.79	1
Maydena	4	25	0	25	0	0	0	0	25	25	0.79	1
CrypNM8	4	25	0	0	0	25	0	0	25	25	0.79	1
Aleohomf	8	50	0	0	0	50	0	0	50	22.4	10.11	0.119

Table 3.23 Potential indicator beetle species for different forest types.

The beetle dataset was reduced from 152 to 49 species to remove rare species whose abundances were too low (less than 5 across all sites) to enable significant indications about associations with particular forest types. Nine beetle species (Table 3.23) were potential indicators of a particular forest type but only *Zeadolopus* NM2 , was statistically significant (p = 0.0140). It was an indicator of WRE.

All Spider species			FOREST TYPE						Observed IV	IV From randomised groups		
	Avg	Max	WRE	WOB	DOB	DTO	DPU	DAM		Mean	S. Dev	p
AMAUNM1	8	44	0	0	3	44	0	4	43.7	20.9	12.61	0.141
GNAPNM3	4	25	0	0	25	0	0	6	25	25	0.79	1
GNAPNM4	4	25	0	0	25	0	0	6	25	25	0.79	1
GNAPNM14	8	50	0	0	0	0	50	5	50	23.8	9.99	0.127
GNAPNM17	8	50	0	0	0	50	0	4	50	17.7	13.03	0.141
GNAPNM36	4	25	0	0	25	0	0	6	25	25	0.79	1

Table 3.24 Potential indicator spider species.

The all spider dataset was reduced from 204 species to 54 to exclude those represented by only 5 individuals or less across all sites. Based on their presence in only one forest type, (Table 3.24) only six species were contenders for indicators of forest type, but none were statistically significant.

4.8.1 Regional variation

The question addressed in this section is whether the variations in species assemblages that were noted in one geographical area can be generalized across much greater distances within the same region. Variation in species assemblages at groups of sites in three widely separated regions 50 km apart (Hobart, Levendale and Swansea) were compared.

Nonparametric Manova tests were conducted with PERMANOVA (Anderson, 2005) for a two-way fixed-factor ANOVA with factors 'Region' and 'Forest type' and a balanced design. There were six replicates. The analysis was based on Bray-Curtis dissimilarities of data transformed to ln (x+1). Results were tested with 9999 unrestricted permutations of the raw data.

Non-parametric Multivariate Analysis of Variance

Variables	Source	df	SS	MS	F	P
Beetles	**Region**	**2**	**9188.5927**	**4594.2964**	**2.4503**	**0.0002**
186 spp	Forest	1	2475.4637	2475.4637	1.3202	0.1936
	RegionxForest	**2**	**11345.4397**	**5672.7198**	**3.0254**	**0.0001**
	Residual	30	56250.8545	1875.0285		
	Total	35	79260.3506			
Spiders	**Region**	**2**	**9129.6481**	**4564.8241**	**1.8352**	**0.0110**
	Forest	1	1455.2956	1455.2956	0.5851	0.9030
(all)	**RegionxForest**	**2**	**9524.2403**	**4762.1201**	1.9145	**0.0070**
	Residual	30	74620.9716	2487.3657		
196 spp	Total	35	94730.1555			
Spiders	**Region**	**2**	**10418.2080**	**5209.1040**	**1.8908**	**0.0150**
	Forest	1	2627.6830	2627.6830	0.9538	0.4900
(adults)	**RegionxForest**	**2**	**11720.7876**	**5860.3938**	**2.1272**	**0.0060**
	Residual	30	82651.1659	2755.0389		
182 spp	Total	35	107417.8445			

Table 3.25 Results of permutational non-parametric multivariate analysis of variance for sampled regional groups. Residuals were used in the denominator of MS for the F-ratio.

There was a significant difference between species assemblages in different regions (p= 0.0002 for beetles, p= 0.0110 for all spiders and p= 0.0150 for adult spiders) (Table 3.25), which pairwise *a posteriori* comparisons (Table 3.26) revealed were consistently due to significant differences between the regions that were furtherest apart, Hobart and Swansea. The intermediate region, Levendale did not host significantly different assemblages.

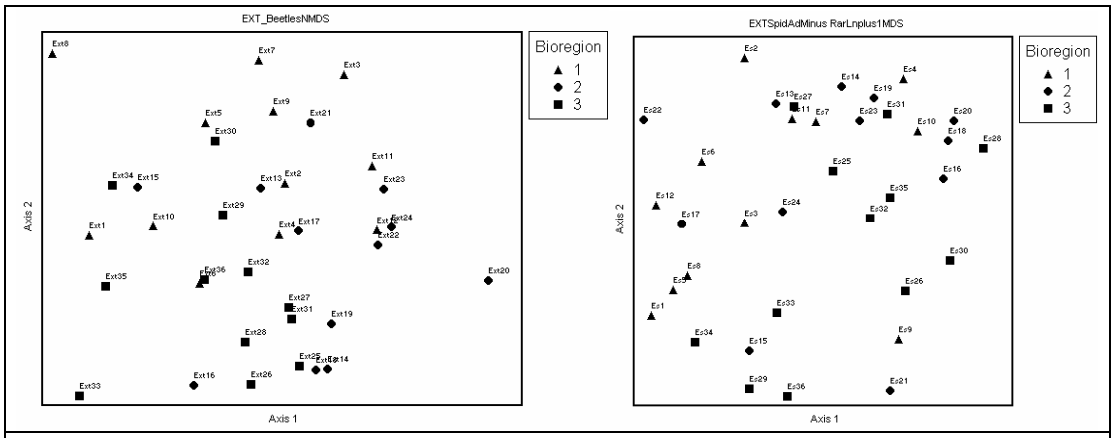
Taxa	Factors	t	P (permut)	P MC	Sig. Level
Beetles	Region (Hbt, Lev)	1.6841	**0.007**	0.019	0.117
	Region (Hbt, Swa)	1.7589	**0.009**	**0.16**	0.025
	Region (Lev, Swa)	1.2271	0.055	0.161	0.05
	Forest by Region: Hbt (DOB, DPU)	1.3097	0.069	0.087	0.05
	Forest by Region: Lev(DOB, DPU)	1.5894	**0.002**	0.012	0.05
	Forest by Region: Swa(DOB, DPU)	1.5048	**0.012**	0.027	0.05
Spiders	Forest by Region: (Hbt, Lev)	0.9055	0.663	0.546	0.05
	Region (Hbt, Swa)	1.5453	**0.033**	**0.034**	0.117
(all)	Region (Lev, Swa)	1.0891	0.267	0.319	0.025
	Forest by Region: Hbt(DOB, DPU)	1.3263	0.06	0.77	0.05
	Forest by Region: Lev(DOB, DPU)	1.6477	**0.003**	**0.008**	0.05
	Forest by Region: Swa(DOB, DPU)	0.9546	0.567	0.519	0.05
Spiders	Region (Hbt, Lev)	1.4443	0.039	0.045	0.025
(adults)	**Region (Hbt, Swa)**	1.6595	**0.005**	**0.007**	**0.117**
	Region (Lev, Swa)	0.809	0.8219	0.736	0.05
	Forest by Region: Hbt(DOB, DPU)	0.9508	**0.513**	0.455	0.05
	Forest by Region: Lev(DOB, DPU)	1.7556	**0.007**	**0.012**	0.05
	Forest by Region: Swa(DOB, DPU)	1.1321	0.222	0.266	0.05

Table 3.26 Results of pair-wise *a posteriori* comparisons for permutational non-parametric multivariate analysis of variance. The significance levels have been Bonferoni corrected for multiple comparisons.

The differences in assemblages in different forest types was not significant for the whole region (p = 0.1936) but when forest types were broken down into regions by *a posteriori* tests (Table 3.26), beetle assemblages were significantly different between forest types in Levendale (0.0090) and Swansea (0.0070). This is supported by a significant multivariate interaction between the factors 'Region' and 'Forest' (p= 0.0001) reported in Table 3.25. Beetles and spider assemblages were significantly different in among forest types DOB and DPU in the Levendale region. None of the multivariate assemblages showed a difference in DOB compared with DPU forest types in the Hobart region and only beetles were significanly different among forest type in the Swansea region.

Nonmetric Multidimensional Scaling methods (NMDS) provided a visual clue to how closely sites from the same region clustered in species space across large distances.

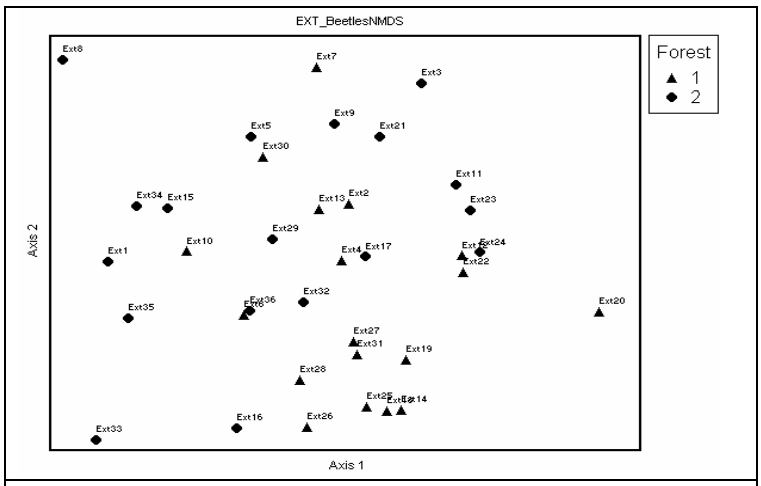
Stress for all plots was very high so they should not be interpreted in detail, but they do portray the failure of sites in the same region to cluster together which demonstrates those sites do not share a greater number of similar species.



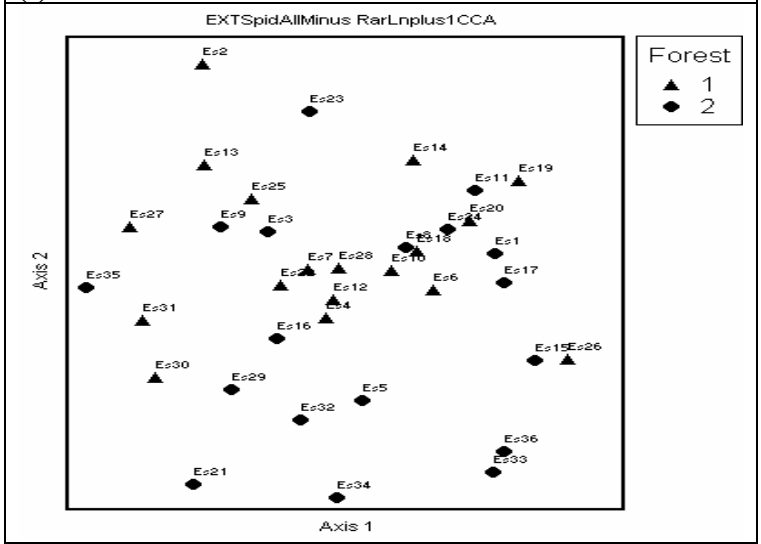
(a) Beetles 1D stress 55.22763 (b) Spider (adult) 3D stress= 19.39610

Figure 3.31 NMDS ordination of regional sites in species space with regional groups indicated: ▲Hobart, ♦ Levendale and ■ Swansea.

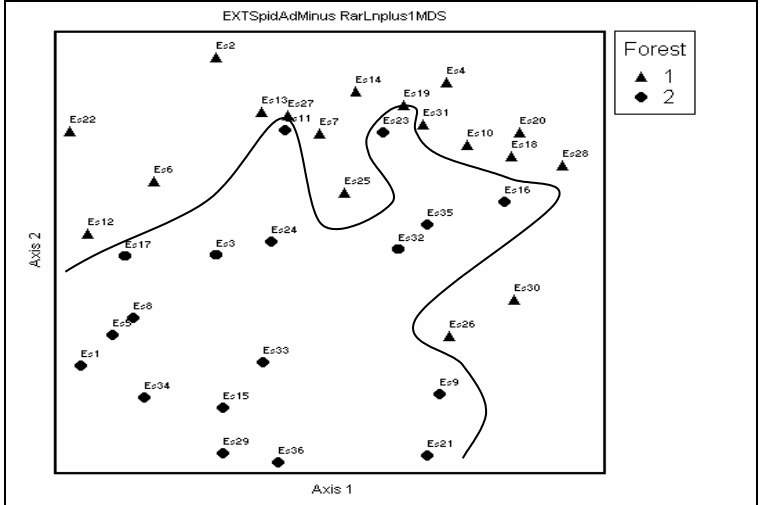
Ordinations of the data demonstrate an overall random stucture of species assemblages which do not correspond to region (Figure 3.31) or forest type (Figure 3.32), though adult spiders do indicate some separation of sites by forest type (Figure 3.32 c).



(a) Beetles 1D stress= 55.2276



(b) Spider (all) 3D stress = 17.627



(c) Spiders (adult) 3D stress= 19.39610

Figure 3.32 NMDS Ordination of regional sites in species space with forest type indicated: ▲DOB and ■ DPU.

4.8.9.1 Regional autocorrelation

The Mantel test results compare dissimilarity in geographic distance between pairs of sites with Bray-Curtis species dissimilarity (Figure 3.33). The value of rho for all assemblages was low, i.e. less than 0.18 (p= 10005), which indicates that sites that were proximate did not necessarily contain a greater number of similar species. This trend was also evident at the scale of the Mt Wellington sites that spanned less than 2 km. The regional sites spanned 157 km with approximately 50km separation between each of the regional groups of sites.

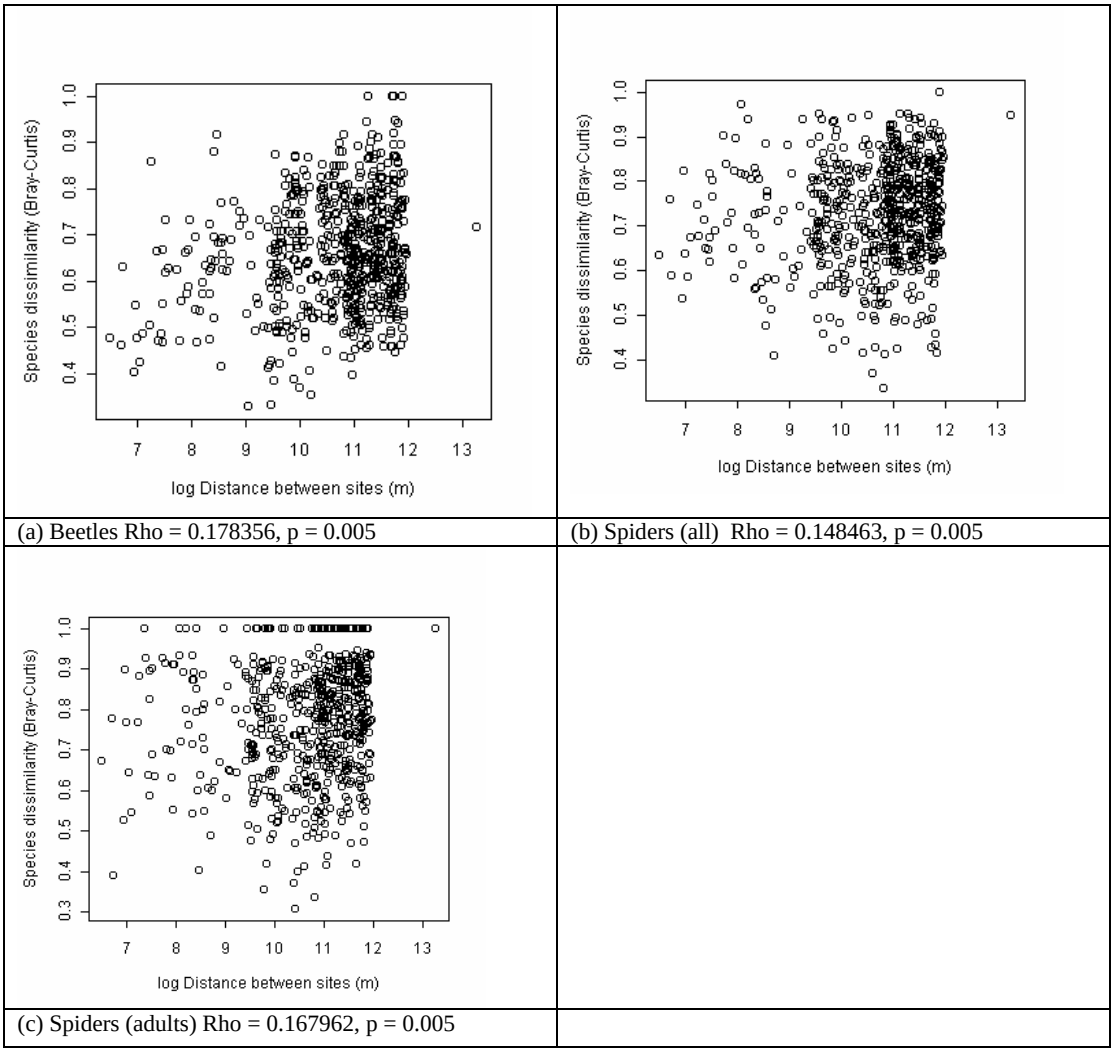


Figure 3.33 Mantel test: Plots of distances between pairs of regional sites against species dissimilarity between pairs of sites (Bray-Curtis) for each of the multivariate species matrices: beetles, spiders (all) and spiders (adults). Spearman's Rank correlation coefficient (rho) appears

under each plot.

4.8.9.2 Similarity between region and forest type

Analysis of similarity in species assemblages between regions and forest types were tested with an ANOSIM function in R with a permutation of dissimilarity ranks from a Bray-Curtis matrix with 1000 permutations. Boxplots of the mean ranks of dissimilarity between and within groups appear in Figure 3.34.

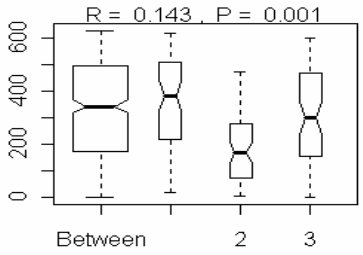
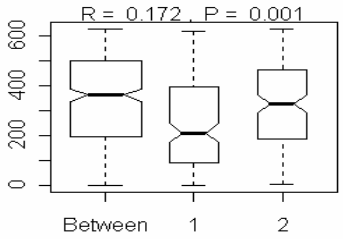
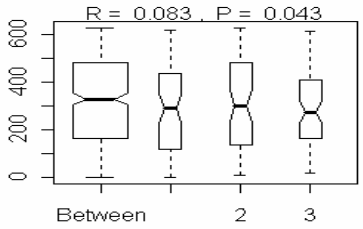
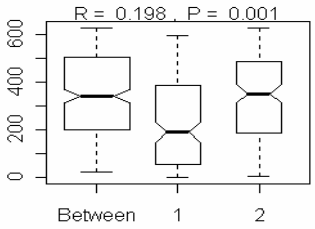
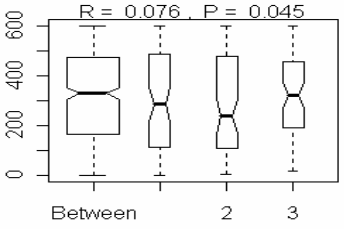
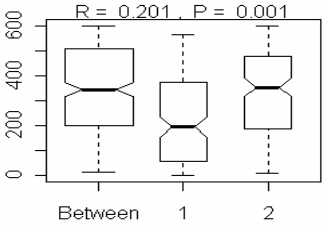
Sites grouped by Region	**Sites grouped by Forest Type**
	
(a) Beetles	(d) Beetles
	
(b) Spiders (all)	(e) Spiders (all)
	
(c) Spiders (adult)	(f) Spiders (adult)

Figure 3.34 The effect of region and forest type on species communities. Boxplots portray mean ranks dissimilarity ranks between and within groups. R range is 1 to -1 (0 = zero similarity).

Key – Region: 1 = Hobart, 2 = Levendale, 3 = Swansea; Forest: 1 = DOB, 2 = DPU.

Boxplots of data classified by forest type (Figure 3.34) portray the wide variation in data as exemplified by the width of the plots. The R values were all significant for each plot. The R values for spider dissimilarity when grouped by Region (left hand side plots) were both close to zero which indicates that there is a strong difference in spider species within regions. The difference was slightly less strong for beetles (R= 0.143). The differences when grouped by forest type were again fairly strong for spiders and beetles with R values around 0.2.

Chapter 4 Discussion

Several themes emerged from statistical analysis of data collected for this study. These themes, discussed below, lead to an understanding of the underlying finer scale of interactions between environment, space and species that are summarised as 'biodiversity', an assessment of which forms the basis for planning decisions.

Many of the statistical tests conducted produced significant results indicating some degree of association between forest type and species. This significance, however, does not imply that distributions of spiders or beetles simply correspond to forest type and illustrates the wrong conclusions that may be drawn from data that are not well interrogated.

Statistical output indicated that some species within assemblages were responsible for these associations while others were not. Thus an assemblage cannot be viewed as a collection of species that interact in the same way and respond in the same way to their environment. This was supported by seasonal variation in species (Figures 3.12 and 3.13 for beetles, and Figure 3.17 for spiders) and investigation of trophic level variation in beetles (Figure 3.14) and hunting styles in spiders (Figure 3.19).

Several tests (NP-MANOVA, CAP and ANOSIM) aimed to find significance in the distribution of multivariate species data grouped by forest type. Each test revealed that association with forest type did not always apply to all species within an assemblage or to all forest types in the study. Each test also revealed different detail about the distribution of each taxa which enabled further exploration as outlined.

NP-MANOVA detected a significant difference between assemblages of beetles and spiders in different mapped forest types ($p= 0.0002$ for each analysis). Pairwise *a posteriori* tests revealed that significant differences were not consistent across all forest types. Complete correspondence of particular assemblages with particular forest

types was lacking.

Beetle assemblages in DTO and DAM were significantly dissimilar to those in wet WRE (p= 0.0291 and p= 0.0316 respectively), WOB (p= 0.0298 and p= 0.0276 respectively) and DOB (p= 0.0262 and p= 0.316 respectively). Assemblages of beetles in DPU were not significantly different to those in any other forest type. An illustration of these relationships appears in Figure 4.1.

In addition WRE also hosted assemblages significantly different to those in DOB (p= 0.0308).

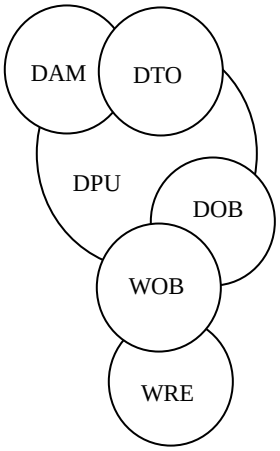


Figure 4.1 Representation of forest types from *a posteriori* NP-MANOVA comparisons of dissimilarity between beetle assemblages in mapped forest types. No overlap of circles represents distinct beetle assemblages

Beetles identified as responsible for multivariate variation from the canonical axes of the CAP analyses were *Nemadini*: Leiodidae, *Scaphidium* sp.:Staphylinidae, *Thalycrodes australe* (Germar, 1848): Nitidulae, *Acrotrichis* sp. (Ptilidae), *Isopteron abscurum* (Erichson, 1842): Tenebrionidae and *Tetrabothrus claviger* (Fauvel, 1878): Staphylinidae.

For all spiders seven species were correlated to some degree with the canonical axes, suggesting they may be responsible for some of the multivariate distribution patterns. They were *Suppuna picta* (Koch, 1873), Gnaphosidae NM34, Gnaphosidae NM37, Micropholcommatidae NM8, Lycosidae NM1, Zodariidae NM26 and Zoridae NM1. It should be observed that these species are all vagrant hunters except

Micropholcommatidae sp. which is a tiny (1.5 mm) web building spider. The distribution of these spiders would be expected to vary according to prey availability and habitat. They all require ground cover such as litter, rocks, coarse woody debris, logs or moss.

There was a general dissimilarity in spider (adults) assemblages from wetter forest types compared to those in drier forest types. However, there was additional separation between the wet sites themselves with WOB dissimilar to all other forest types. This suggests that important factors are more complex than a simple moisture gradient. Wet WRE was significantly dissimilar to all other forest types except dry DOB which was nearly significantly different ($p = 0.0564$). These relationships are illustrated in Figure 4.2. The distribution of only one adult spider species, *Hestimodema* A (Zoridae) correlated with any significance with the canonical axes. *Hestimodema* A is another vagrant hunter that lives under litter, rocks, coarse woody debris or logs.

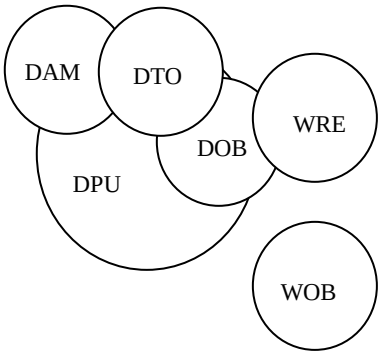


Figure 4.2 Representation of forest types from *a posteriori* NP-MANOVA comparisons of dissimilarity between spider assemblages in mapped forest types. No overlap of circles represents distinct spider (adults) assemblages.

Examining the dispersion of the data was valuable in determining the extent to which the significant effects of forest type found in NP-MANOVA were due to differences in location or differences in spread of the data (Anderson, 2004).

Multivariate dispersion of the adult spider data was not significantly different among groups of forest type (p= 0.5271), so forest type itself had an effect on assemblages to the extent revealed by the *a posteriori* NP-MANOVA comparisons discussed above. Mutivariate dispersion of the beetle data was significant (p= 0.0244) which means that there was a significant amount of dispersion in the beetle data between groups so forest type *per se* did not necessarily account for the significant NP-MANOVA results. Once again, significant effects cannot be assumed to be the same across all forest types studied as shown by DTO forest type which seemed to be largely responsible for the dispersion. One conclusion of this analysis is that high dispersion due to high variation in assemblages within a particular forest type implies that factors other than forest type are influencing species distributions.

Canonical analysis of Principal co-ordinates (CAP) with discriminant analysis (DA) indicated that forest type was not significant for beetles, (the very low squared canonical correlation (δ^2) of 0.069088 which was not significant (p= 0.8558)).

Forest type was highly significant for all spiders, with δ^2 = 0.909598 (p= 0.0011) but was no longer significant when only adult spiders were considered (squared canonical correlation (δ^2 = 0.385911, p= 0.3944).

The leave-one-out cross validation test had generally poor success in correctly allocating species to forest type, suggesting high variability in assemblages in most forest types, see Table 3.18. Successful beetle allocation was highest (75%) for WOB and DAM and lowest for DOB and DPU (25% and 0% respectively).

All spiders in forest type WRE were correctly allocated (100%) with high allocations (75%) for WOB and DOB. Zero successful allocation of all spiders to DPU and DAM reinforce the finding that spider assemblages are highly variable in these forest types. When only adult spiders were considered, they were successfully allocated (75%) to

WRE WOB and DAM but were unable to be successfully allocated (0%) to DOB. Again differences in distributions of species are revealed when juveniles are included with adult spiders.

Canonical correlation of species distribution and environmental variables provided some interesting insight into the adequacy of the environmental variables measured because they were thought *a priori* to be important. The resulting subset of beetles most highly correlated with forest type alone was dominated by fungivores: *Nemadini*, *Thalycrodes australe* (Germar, 1848), *Acrotrichis* sp. and *Scaphidium* sp. (Table 4.1).

	Correlated with Forest type	Correlated with Environmental variables
beetles	**Nemadini** ***Thalycrodes australe*** *Acrotrichis* sp. ***Scaphidium* sp..** *Isopteron obscurum* *Tetrabothrus claviger*	**Nemadini** ***Thalycrodes australe*** *Thalycrodes cylindricum* ***Scaphidium* sp.** Zead NM2 *Rybaxis rugosus* *Mandalotus* NM1 *Anotylus B*
Spiders (all)	*Suppuna picta* Gnaphosidae NM34 Lycosidae NM1 Micropholcommatidae NM8 Zodariidae NM26 Zoridae NM1	*Suppuna* NM1 Gnaphosidae NM1 Laetesia NM1 Mynogleninae NM33 *Storena flavipes* Zodariidae NM12

Table 4.1 Species whose distribution was found, by canonical analysis of principal coordinates, to be correlated with forest type (column 2) or with the set of environmental variables (column 3).

The appearance of some beetles in both lists suggests that they might respond to environmental variables that are correlated with forest type, for example canopy cover; or they might respond to other environmental variables in addition to forest type. Earlier, *Isopteron obscurum* (Erichson, 1842) and *Tetrabothrus claviger* (Fauvel, 1878) were identified among those whose distribution corresponded to forest type to some degree. The current analysis separates them from the others in that list (Table 4.1) which were all fungivores. This means that none of the environmental variables measured in this study significantly explained their distribution beyond

forest type. Since the correlation of canonical axes with the species distribution was 0.6621 and 0.6381 respectively, there are still unknown variables contributing to their distribution beyond those in this research.

It is possible to represent these associations of beetles as follows (Figure 4.3):

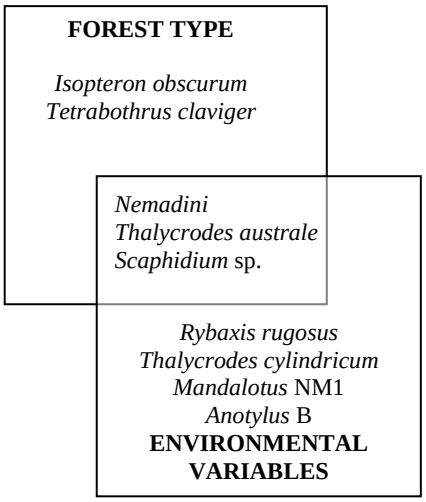


Figure 4.3 Representation of beetles whose distributions, from canonical correlation, are correlated with mapped forest type or measured environmental variables or both.

Some beetle species that were correlated with environmental variables were not highly correlated with any of the canonical axes discriminating among forest type, namely *Rybaxis rugosus*, *Thalycrodes cylindricum* Blackburn, 1891, *Mandalotus* NM1 and *Anotylus* B.

PCA analysis of environmental variables produced a reduced set of variables that corresponded to most to differences between sites. BIOENV identified a similar set of variables that correlated strongest with the biotic data (Table 3.21). NMDS ordinations (Figure 3.25) provided a basis for distinguishing among the effects of the variables by indicating environmental gradients which are summarised in Figure 4.4.

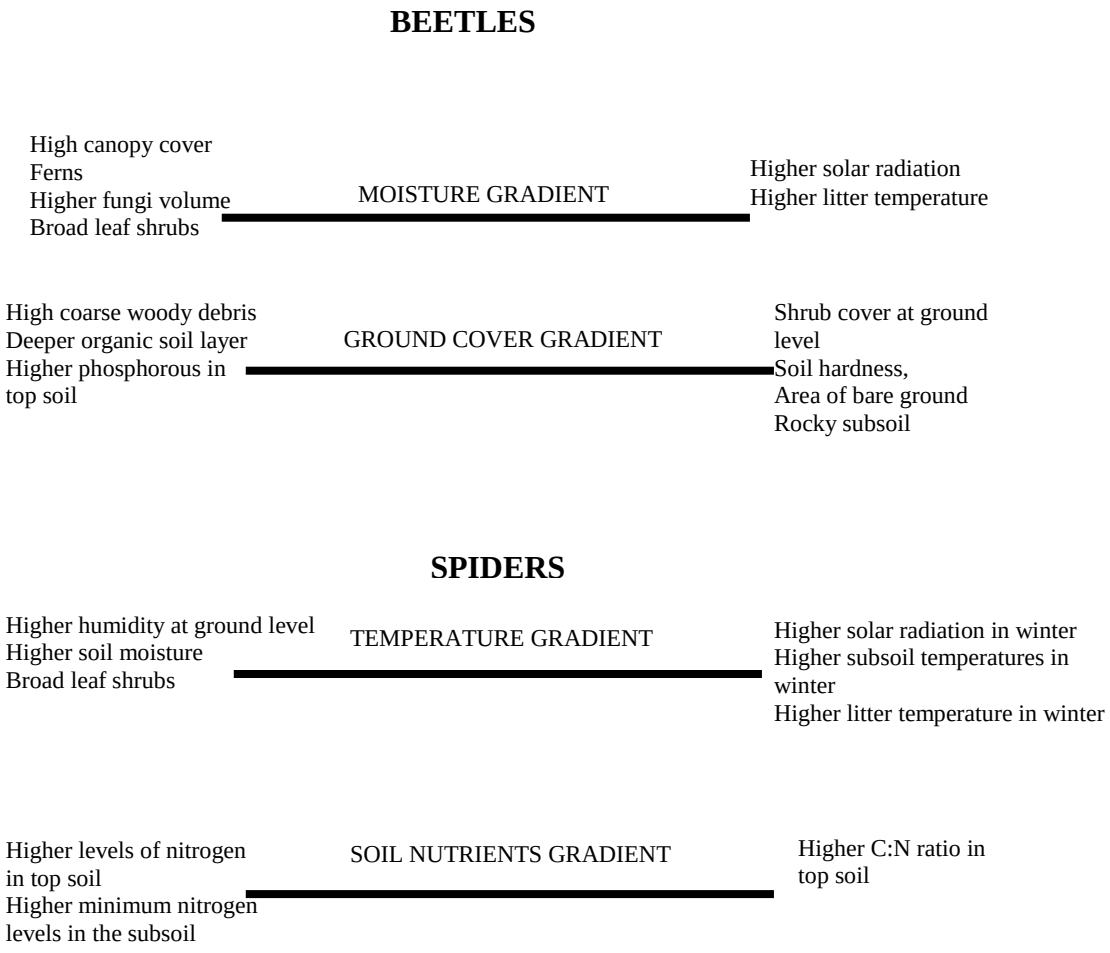


Figure 4.4 Diagrammatic representation of environmental gradients identified as associated with beetle and spider assemblages.

Beetles seemed to correspond to a moisture gradient which, at the wetter end, most strongly correlated with canopy cover and created a microclimate suitable for increased fungi volume, ferns and broad leaf shrubs. Canopy cover and soil moisture have been identified by other researchers as variables that affect the distribution of beetles (Magura 2002; Niemela and Spence 1994; Oliver *et al.* 2000). The finding that beetle species richness was lower in the more open canopy of the drier forests and higher under the more closed canopy of wetter forests (Figure 3.20) supports results

of Oliver *et al*. 2000. Oliver *et al*. (2000) also found that ants, like the spiders in this research, had an inverse relationship to canopy cover compared with beetles, and displayed lower species diversity in wet forests and increased diversity under low canopy cover. Environmental variables such as ground temperature, surface temperature, air moisture, cover of leaf litter, herbs, shrub and canopy layer have been identified as significant for carabids (Magura 2002).

Variables not measured which are likely to be associated with this environment gradient include mosses and lichens which host a number of beetles from families found in this study such as Byrrhidae species (Lea 1920), weevils e.g. *Mandalotus bryophagus, Mandalotus carinativentris* (Lea 1907) and Scydmaenidae e.g. *Scydmaenus seminiger, Phagonophana suturalis* (Lea 1914) and Pselaphids e.g. *Euplectops bryophilis* Lea, 1911, *Sagola tasmaniae* Lea, 1911 and *Schistodactylus brevipennis* Lea 1911 (Lea 1911). A moist microclimate would increase presence of litter herbivores which may be prey for predatory beetles. The microclimate would also increase litter fungi which would sustain fungivorous beetles such as *Thalycrodes* spp., Leiodidae and Lathridiidae. The drier end of the gradient was associated with higher solar radiation on the ground (due to lower canopy cover), and higher litter temperature. A ground cover gradient was identifiable for beetles where increased ground cover was associated with high levels of coarse woody debris, increased depth of top soil and higher levels of phosphorus in the top soil. These findings support those of Oliver *et al*. (2000) who identified similar variables such as percent cover of subcanopy and the cover of the ground layer (litter depth, bare soil and rock) that explained significant variation in ground beetles and spiders. Several beetle families have an obligate association with CWD (Dajoz 2000; Grove 2002, Yee *et al.* 2001), including Buprestidae, Cerambycidae, Bostrichidae, Brentidae and the Curculionids Scolytinae and Platypodinae (Ulyshen *et al*. 2004), while Leiodidae feed on fungi and slime moulds associated with CWD (Chandler and Peck 1992).

Spiders were correlated with a moisture gradient that separated spiders associated with higher humidity at ground level, higher soil moisture and broad leaf shrubs at one end from higher radiation at ground level (due to less canopy cover), higher

subsoil temperatures in winter and higher litter temperature in winter. The higher temperatures variables would favour active spiders such as vagrant hunters. A second gradient, soil nutrients, associated spiders in wetter sites with higher levels of nitrogen in the top layer of soil (A horizon) and higher minimum levels of nitrogen in the subsoil (B horizon). Spiders in the drier sites were associated on the soil nutrient gradient with a higher carbon to nitrogen ratio in the top soil layer (A horizon).

It may seem curious that distributions of spiders and beetles might correspond to soil nutrients, however available phosphorus levels are known to increase following nest material accumulation by ants (Frouz *et al*. 2005; Kristiansen *et al*. 2001), and passage of organic material through the gut of soil macrofauna such as scarab beetle larvae (Li *et al.* 2006) and earthworms (Sharpley and Syers 1977). Beetles associated with raised levels of phosphorus are likely to be predators of soil macrofauna such as ants and beetle larvae that are active in raising these nutrient levels. The more numerous predatory litter beetles in this study include *Notonomus politulus* (Chaudoir, 1865): Carabidae.

Soil nitrogen levels are increased by several factors including ant activity in nests (Lenoir *et al.* 2001), litter herbivore activity (Chapman 2003; Hunter *et al*. 2003) litter bacteria and litter and wood-rotting fungi (Lindahl *et al*. 2007). Increased nitrogen lowers the C:N ratio. Spiders associated with raised levels of N may be predators of ants, litter herbivores and fungivores and in this study would include vagrant hunters in the families Corrinidae, Lycosidae and Clubionidae, as well Linyphiidae which, as web spinners, build small webs on structural elements at ground level, including rocks and stones (Nentwig 1980) and are particular predadators of collembola. Several dry sclerophyll plant species in this research such as eight *Acacia* spp., *Daviesia ulicifolia* and five *Pultenaea* spp. are amongst those known to contain root nodules that host symbiotic microrganisms that fix nitrogen and increase its availability to the environment (Bowen 1986). There may be associations between some vagrant spiders and sources of prey that inhabit these species of plants.

The variation in environmental variables between beetles and spiders indicate different uses of their habitat. For example the volume of rotting wood was amongst the most highly correlated variables for spiders and beetles (Table 3.21). At the ecological level this suggests a correlation with beetle species that breed in and feed on rotten wood (saprophages). Spider species inhabiting rotten wood may be specialised predators of occupants of rotten wood.

The absence of certain species of beetles in the relatively undisturbed habitat fragments sampled in this study were consistent with findings from other studies (Baker 2006; Grove and Yaxley 2005; Michaels and McQuillan 1995; Michaels 1999). Beetles associated with regenerating forests, were present only as a singelton (*Mecyclothorax ambiguus* (Erichson, 1842) or absent (*Scopodes sigillatus* Germar, 1848 and *Rybaxis parvidens* Lea, 1911) (Baker 2006; Michaels and McQuillan 1995; Michaels 1999). *Notonomus politulus* (Chaudoir, 1865), a specialist of old-growth forest (Michaels and McQuillan 1995) was found in this study.

Little is known of the ecology and distribution of many beetles and, more particularly, spiders. For example, two spider species of the Nicodaemidae family that are known to be widely spread in Tasmanian forests, were found in this study - *Ambicodamus sororius* (Harvey, 1995) and *Novodamus nodatus* (Karsch, 1878). *N. nodatus* is described as an inhabitant of closed wet forest where its habitat includes underneath stones, under bark of eucalypts and dead wattles, shrubs and litter (Harvey, 1995). In this study both species were found at sites in dry eucalypt forest types with less than 50% canopy cover and a third, unnamed, species of Nicodaemidae was also found. In the extensive study Nicodaemidae were only found in *E. pulchella* forest in the Levendale region with *A. sororius* totally absent from the regional samples. With so little known about species it is difficult to predict their distribution. This research aimed to reveal some variables that enable distributions of invertebrates to be predicted as an aid to the planning of reserves.

Species richness differences in similar habitats are frequently indicators of disturbance (Broque and Buckney 2003; Gibb and Hochuli 2002; Harris *et al.* 2003) or pollution (Clarke and Ainsworth 1993; Deeleman-Reinhold 1990) but are not a viable basis for selection of terrestrial reserves across a landscape where differences in composition of assemblages must be considered (Su *et al.* 2004). Spiders in this research, for example, were more diverse in dry forest types, but their species diversity was lower yet significantly different in wet forest types. Species would be lost if wet forests weren't also reserved.

Planners have focused on the objective of reserving a *representative* diversity of species which has been tackled in a variety of ways. A minimum representation goal has derived site scores from multiple criteria such as species diversity and rarity, condition and area of habitat etc to provide a priority index to identify the minimum number of sites required to maximize reserved biodiversity (Possinghham *et al*. 2000; Pressey and Nicholls 1989). A similar complimentarity approach (Faith and Walker 1996; Faith et al. 2003; Justus and Sarkar 2002; Oliver *et al.* 1998) iteratively reweights attributes of species occurrences or habitats as sites become prioritised for reservation so that additional sites contain attributes not already reserved (Bedwood *et al*. 1992; Kirkpatrick 1983; Possingham *et al.* 2000) based on the composition of assemblages and inclusion of rare species (Margules 1989). Algorithms used to create site scores have been based on subjectively differently measured parameters, pattern analysis (McKenzie *et al.* 1989) and statistically derived regression models based on correlated variables (Lindenmayer and Cunningham 1996; Margules and Stein 1989). Different methods have created variable results when ranking sites for reserves (Kirkpatrick 1983; Margules and Stein 1989: Possingham *et al.* 2000; Pressey and Nicholls 1989) and selection of the minimum reserve set is not necessarily sufficiently robust under temporal species turnover where local extinctions may occur (Rodriges *et al*. 2000).

The minimum representation focus on planning has been largely descriptive of the biotic and abiotic features at the time they were measured or assessed. At the same

time collection of data on changes in species distributions is costly and time consuming. One tool which has become useful to planners considering reserves in a fragmented landscape is the minimum fragmentation threshold which is a measure of habitat area below which a species may be lost (Drinnan 2005). Its value has been questioned (Hugget 2005; Lindenmayer *et al*. 2005; Lindenmayer and Luck 2005) as perhaps encouraging no more than a minimum area to be reserved while the minimum habitat size will depend upon the condition if the remnant (McCoy and Mushinsky 2007). Environmental domain analyses (Belbin 1993; Mackey *et al.* 1988) based on 'ecologically relevant environmental variables' as surrogates for species distribution data (Kirkpatrick and Brown 1994) have been successfully applied to vegetation data and are a basis for GIS modelling of potential habitat of specific species and spatial prediction using geostatistics (Cabeza *et al.* 2004; Dettmers and Bart 1999; Hengle 2007).

Modelling has been attempted across scales from point collected species data which are affected by fine scale environmental changes to the macro-scale of landscapes and their connectivity (Urban 2005). An increasing focus on landscape ecology faces planners with challenges as they consider biodiversity across the broader landscape which is not static and where land clearing, fire, habitat fragmentation and so on are altering biotic and abiotic dynamics. Landscape metrics that characterise landscape patterns are being refined to provide information for modelling landscape processes (Debuse *et al.* 2007; DiBarri 2007; Hargis *et al.* 2004; McAlpine and Eyre 2002) including scaling equations (Wu *et al*. 2002). It was difficult for the current research on spiders and beetles to identify patch-scale variables that accounted for most of the variation in assemblages. This emphasises the difficulty in achieving adequate landscape-scale metrics. The challenge is to identify non-redundant variables whose gradients are highly variable and therefore useful for distinguishing between different landscapes. Predictive models that enable scenario planning frequently make use of Bayesian paradigms (Calder *et al.* 2003; Clark 2005; Hobbs and Hilborn 2006) using probability distributions of measured parameters (Borsuk *et al.* 2001; Kerman and Gelman 2007; Latimer *et al*. 2006; Martin *et al.* 2005) and qualitative predictions

(Dambacher *et al.* 2003).

It should also be recognised that the scale of impact from threatening processes such as land clearing and habitat fragmentation is much larger for invertebrates (Hutchings and Ponder 1999) and we must not lose sight of the purpose for reserving biodiversity, which is to build the resilience of ecosystems to survive threatening processes.

4.8.1 Regional variation

The measure of species diversity at different geographic scales was found to vary considerably, which supports the view that different species respond to habitat at different spatial scales (Holland *et al.* 2004; Yaacobi and Ziv 2007). Assemblages were sampled in three regions approximately 50 km apart and provided a comparison of diversity at the local scale of 1km in the Mt Wellington study with differences in species present regionally at the scale of fifty kilometres, and for the entire region sampled, at the scale of 150 kilometres. Using a modified Whittaker's beta diversity index, it was observed that beta diversity was higher for beetles and spiders (25 and 29 respectively) than for plants (7) and fungi (15) at the local scale of a kilometre (Table 4.2). The beta diversity of beetles and spiders was highest at the scale of 50 km (range from 30 to 42), and lowest at the scale of 150 km (range 16 to 19) (Table 4.2).

	diversity index		
Taxa	Local scale (1km)	Regional scale (50km)	Extensive scale (150 km)
beetles	24	36 - 40	19
spiders (all)	29	29 - 38	16
Spiders (adults)	29	30 - 42	17
Fungi	15	n/a	n/a
Plant spp.	7	n/a	n/a

Table 4.2 Variation in beta diversity measured at different scales. n/a means data was not available at the regional scale.

The low beta diversity in plants was not reflected by invertebrates for which there were large differences in assemblages. This provides evidence that plants and

invertebrates need to be considered differently when planning for conservation of biodiversity (Mesibov 1993; Oliver *et al.* 1998). Geographic distances at which measures of diversity are applied must also be recognised.

Spiders and beetles demonstrate some differences in their distributions and may be the case that when this data is analysed against concurrently collected ant data (Meeson 2006) that further different distributions of invertebrate assemblages are identified. Oliver and Beattie (1996), for example, recommend that ant and beetle data be combined for an accurate characterisation of invertebrate assemblages. Oliver *et al.* (2000) conclude that ant richness has more potential than beetle richness as a performance indicator of sustainable forest management because ant assemblages can be more accurately and quickly represented by pitfall sampling because of their higher foraging activity compared with beetles.

Non-parametric multivariate analysis of variance indicated that there was a significant difference in assemblages between the Hobart and Swansea regions (Table 3.25), with overlap of species in the intermediate Levendale region. When regions were considered together, at the scale of 150 km, assemblages were not significantly different between the two forest types (DOB and DPU), but when considered by region, assemblages in different forest types were significantly different between Swansea and Levendale. The differences in assemblages in DOB and DPU forest types were also not detectable at the local scale of 1km (Tables 3.13 and 3.15). This indicated that the scale of 50 km was the resolution at which the more subtle differences between assemblages in different dry forest types could be detected. The possibility of creating connectivity within forest types studied in this research would be challenging due to their patchy, limited distribution (Figure 2.3) and threats from loss of dry eucalypt forests to fuelwood, logging, land clearing for agriculture and coastal development (Brown and Podger 1999; Williams 1991). Keitt *et al.* (1997) present a method for quantifying conservation priority of fragmented habitat patches that contribute most to connectivity, based on dispersal abilities of species, connection probabilities and percolation theory.

4.8.1 Including juvenile spiders in ecological studies.

It is possible to include juvenile spider data if a family level of resolution of a spider sample is required (New 1999) since, for some research questions, family level analysis is adequate (Churchill 1995). It is more usual to exclude juvenile spiders from samples because of the difficulty in identifying them to species level (Coddington *et al*. 1996; Harris *et al*. 2003; Oxbrough *et al.* 2005; Uetz 1977). A third (34%) of all spiders sampled in this study were juveniles with statistical analyses conducted on 'all spiders' sampled and 'adults only'. The purpose was to explore the possibility that the inclusion of juveniles may provide more power for statistical analysis.

The inclusion of juveniles created 17 families in addition to the 183 families of adults. Each family of exclusively juvenile spiders was represented by a maximum of three individuals, and more usually one or two individuals. These families were routinely excluded from analyses where rare species (represented by less than five individuals) are not included because their abundance is insufficient to show any distribution patterns. The inclusion of juveniles with identified adults would have been a source of error by inflating abundance of certain species even though a fairly strong ln (x+1) transformation of data was usually selected to reduce dominance of abundant species.

Results of analyses varied depending on whether juveniles were included or not. For example, the inclusion of juvenile spiders reduced the correlation of spiders with forest type from R = 0.417 to R = 0.396 and increased the variability of assemblages between sites within the same forest type (see boxplots Figure 3.22). Adult spiders showed a stronger significant association with a larger number of environmental variables than when juveniles were included (Table 3.21). Variables not significant when juveniles were included were shrub cover, soil hardness and volume of rotting wood. This could be due to a number of factors related to dispersal mechanisms

among spiders whereby juveniles are found in a larger range of microhabits that they may traverse before selecting a suitable niche. The fact that they were sampled at a particular site does not imply an association. Alternatively, use of habitat or activity level may vary during the lifecycle of some species. Seasonal variation in abundance of juvenile spiders (Figure 3.17) shows a decrease in the summer which, apart from natural losses through competition and predation, may be due to maturation. Certainly when making cross-taxon comparisons of pitfall sampled beetles, ants and so on it is usually adults that are compared (Gibb and Hochuli 2002; Major *et al.* 1999; Oliver *et al.* 1998).

Therefore, rather than excluding juvenile spiders from research results because they present taxonomic problems, this research provides statistical analysis that points to ecological reasons for their exclusion.

Textricella hickmani Forster, 1959
Micropholcommatidae
(adult male)

Phoroncidia sp.
Theridiidae
(juvenile male)

Micropholcomma sp.
Micropholcommatidae
(adult male)

Chapter 5 Implications and Conclusion

This study contributes to knowledge about the distribution of litter spiders and beetles. In relation to the original objectives, the research was able to describe the assemblages of spiders and beetles in six different eucalypt forest types in Tasmania and their relationship with a range of measured environmental variables. A number of statistical tests found that forest type was a variable that affected the distribution of beetles and spiders but that this varied with different forest types and was not sufficient to fully explain the complex patterns in their distribution.

A suite of variables including canopy cover and spatial separation, were identified that were able to predict a variation in species composition better than vegetation alone. At the scale of beetles and spiders living in the litter on a forest floor, any particular forest type is not homogenous and can provide a variety of microhabitats to which species respond.

Environmental gradients were identified that explained some of the variation in distribution of the two taxa. Beetles such as saprophytes and fungivores (Leiodidae, Nitiduale, Staphylinidae etc) responded to a moisture gradient created by higher canopy cover that harboured increased broad leaf shrubs, ferns, and a greater volume of fungi. At the dry end of the gradient where lower canopy cover increased solar radiation and litter temperature, were weevils (Curculionidae) and ground beetles (Carabidae). The second environmental gradient for beetle distribution was ground cover, with high amounts of coarse woody debris deeper top soil and higher levels of phosphorus in the organic layer at one end. The other end was characterised by shrub cover at ground level, soil hardness, increased area of bare ground and subsoil rock.

Spiders responded to a moisture/temperature gradient and soil nutrient gradient. Parameters of the moisture gradient for spiders were higher air humidity at ground

level, higher soil moisture and broad leaf shrubs. At the dry end, significant variables were higher subsoil and litter temperatures in winter, and increased winter solar radiation due to less canopy cover. The soil nutrient gradient was separated between higher minimum levels of nitrogen in the subsoil and organic layer at one end and a higher C: N ratio in the organic layer at the other end.

Characteristic assemblages associated with any of the particular forest types were not identifiable and only one indicator species was identified, a beetle species, *Zeadolopus* sp. that was associated with the wet WRE forest type.

Variation in diversity occurred when measured at different scales and at the resolution of 50 km differences in assemblages could be detected in different forest types. If planning is to include mapped forest types, then this indicates that a mosaic of vegetation based reserves may need to consider this scale of 50 km as a maximum separation distance between patches of the same forest type in order to capture the change in diversity in spider and beetle species across a landscape. These distances would need to be tested with other taxa.

This research reveals that the interaction between environmental variables and beetles and spiders is complex and highly variable. Other researchers have also been unable to explain a large amount of variation in arthropod assemblages using variables chosen *a priori*. Oliver *et al.* (2000), for example, found that variables explained less than 20% of variation in ant and selected beetle families.

It would have been useful to have found surrogate environmental measures that could improve the prediction of species composition of assemblage composition of litter beetles and spiders by forest type alone. Unfortunately this was not the case. A major insight is that while connections can be made for some groups within each taxa, the

species within each are so highly variable that examination at the assemblage level provides no clear prescriptions for managing the reservation of invertebrates but may indicate variables that will help refine landscape metrics and modelling to predict species occurrences.

Decilaus sp.
(Curculionidae)

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APPENDICES

APPENDIX 1. Mt Wellington site details

Site No.	Eucalypt Forest Type	TAS VEG 2000 code	TASVEG code v 1.2 2005	GDA94 Easting (AGD66)	GDA 94 Northing (AGD66)	Aspect (degrees)	Slope (degrees)	Altitude (metres)
1	*E. regnans* forest	R	WRE	521650 (521762)	5252200 (5252383)	120	19	290
2	*E. regnans* forest	R	WRE	521162 (521274)	5252070 (5252253)	40	22	340
3	*E. regnans* forest	R	WRE	521301 (521413)	5251967 (5252150)	80	11	320
4	*E. regnans* forest	R	WRE	521369 (522147)	5251895 (5252078)	20	17	290
5	*E. obliqua* forest with broadleaf shrubs	OT	DOT	522035 (522449)	5251663 (5251846)	190	26	260
6	*E. obliqua* dry forest	O	DOB	522337 (522449)	5251772 (5251955)	120	17	270
7	*E. obliqua* forest with broadleaf shrubs	OT	WOB	522541 (522653)	5251842 5252025)	140	17	250
8	*E. obliqua* dry forest	O	DOB	522011 (522123)	5251965 (5252148)	360	19	230
9	*E. tenuiramis* forest on sediments	TI	DTO	521892 (522004)	5251761 (5251944)	360	14	290
10	*E. tenuiramis* forest on sediments	TI	DTO	522388 (522500)	5252052 (5251955)	320	17	300
11	*E. pulchella* forest	P	DPU	522716 (522828)	5252070 (5252253)	300	11	280
12	*E. obliqua* forest with broadleaf shrubs	OT	WOB	522861 (522973)	5251879 (5252062)	150	22	230
13	*E. pulchella* forest	P	DPU	522769 (522881)	5252026 5252209)	190	11	290
14	*E .amygdalina* forest on mudstone	AI	DAM	522861 (522973)	5252195 (5252378)	320	11	280
15	*E .amygdalina* forest on mudstone	AI	DAM	522784 (522896)	5252284 (5252467)	340	6	250
16	*E. obliqua* forest with broadleaf shrubs	OT	WOB	522855 (522967)	5252538 5252721)	110	17	220
17	*E. obliqua* dry forest	O	DOB	522747 (522859)	5252565 (5252748)	100	14	240
18	*E. pulchella* forest	P	DPU	522608 (522720)	5252255 (5252438)	70	17	260
19	*E. tenuiramis* forest on sediments	TI	DTO	522569 (522681)	5252494 (5252677)	300	11	270

20	*E. obliqua* dry forest	O	DOB	522150 (522262)	5251936 (5252119)	270	19	250
21	*E. tenuiramis* forest on sediments	TI	DOT	522300 (522412)	5251928 (5252111)	270	19	310
22	*E. amygdalina* forest on mudstone	AI	DAM	522559 (522671)	5252740 (5252923)	300	24	220
23	*E. amygdalina* forest on mudstone	AI	DAM	522424 522536)	5252585 (5252768)	240	19	220
24	*E. pulchella* forest	P	DPU	522428 (522540)	5252355 (5252538)	290	19	250

2. Regional site details

site no	site name	region	forest code	forest type	easting AGD66	northing AGD66	Easting GDA94	Northing GDA94	map alt	alt source map	aspect	aspect index	% canopy cover	mean soil pH	mean slope
1	Chicks Perch	Hobart	1	P	507745	5237630	507857	5237813	360	1:25k topo	290	26	39	6.3	15
2	Dowlings Rd	Hobart	2	O	506840	5238164	506952	5238347	200	1:25k topo	140	176	52	5.9	18
3	Pelverata	Hobart	1	P	508042	5232781	508154	5232964	130	1:25k topo	220	96	43	6.5	20
4	Herringback	Hobart	2	O	511986	5239157	512098	5239340	460	1:25k topo	10	56	54	6.1	9
5	Conningham	Hobart	1	P	523397	5229215	523509	5229398	100	1:25k topo	10	56	44	6.7	17
6	Snug Falls	Hobart	2	O	518078	5229663	518190	5229846	270	1:25k topo	280	36	50	5.1	16
7	Truganini	Hobart	2	O	528837	5246687	528949	5246870	80	1:25k topo	160	156	55	5.9	26
8	Uni Reserve	Hobart	1	P	525609	5248854	525721	5249037	250	1:25k topo	20	66	26	6.4	13
9	Ridgeway	Hobart	1	P	523890	5248210	524002	5248393	300	1:25k topo	220	96	35	6.1	17
10	Huon Rd	Hobart	2	O	523441	5249537	523553	5249720	230	1:25k topo	140	176	59	6.1	16
11	Mount Wellington s18	Hobart	1	P	522608	5252255	522720	5252438	260	1:20k mt well	70	116	41	5.9	17
12	Mount Wellington s8	Hobart	2	O	522011	5251965	522123	5252148	230	1:20k mt well	360	46	48	6.5	19
13	Black Hills O south	Levendale	2	O	548534	5272525	548646	5272708	350	1:25k topo	220	96	51	6.1	22
14	Black Hills O north	Levendale	2	O	549256	5272931	549368	5273114	390	1:25k topo	360	46	53	6	10
15	Black Hills P north	Levendale	1	P	552180	5272858	552292	5273041	320	1:25k topo	30	76	35	6.7	13
16	Black Hills P south	Levendale	1	P	549589	5271020	549701	5271203	320	1:25k topo	200	116	53	6.4	16
17	Mosquito Marsh	Levendale	1	P	545754	5286456	545866	5286639	340	1:25k topo	300	16	29	6.9	17
18	Country Marsh Rd O north	Levendale	2	O	541956	5295569	542068	5295752	540	1:25k topo	360	46	50	6.3	9
19	Country Marsh Rd O south	Levendale	2	O	545168	5292925	545280	5293108	580	1:25k topo	250	66	50	5.2	6
20	Tiger Point O	Levendale	2	O	544266	5290383	544378	5290566	440	1:25k topo	140	176	57	6.8	17
21	Brown Mtn South	Levendale	1	P	542034	5282954	542146	5283137	570	1:25k topo	200	116	46	6.5	15
22	Mother Rough O	Levendale	2	O	543376	5285922	543488	5286105	490	1:25k topo	280	36	55	6.3	21
23	Mother RoughP south	Levendale	1	P	544166	5285719	544278	5285902	520	1:25k topo	120	166	39	6.6	20
24	Mother RoughP north	Levendale	1	P	544062	5286754	544174	5286937	530	1:25k topo	10	56	47	6.4	11
25	Harding Falls	Swansea	2	O	590982	5366145	591094	5366328	280	1:25k topo	150	166	60	6.2	12
26	MS Road Quarry	Swansea	2	O	582627	5364661	582739	5364844	420	1:25k topo	30	76	57	6.7	18
27	MS Road O north	Swansea	2	O	579204	5362194	579316	5362377	380	1:25k topo	50	96	54	6.2	11
28	MS Road O south	Swansea	2	O	579218	5360798	579330	5360981	340	1:25k topo	100	146	62	6.3	21
29	McNiells Rd P north	Swansea	1	P	577367	5335317	577479	5335500	360	1:25k topo	310	6	45	6.9	25
30	McNiells Rd O north	Swansea	2	O	574236	5334747	574348	5334930	550	1:25k topo	360	46	46	6.7	8
31	McNiells Rd O south	Swansea	2	O	576784	5333677	576896	5333860	420	1:25k topo	200	116	47	6.6	11
32	McNiells Rd P south	Swansea	1	P	575965	5334497	576077	5334680	510	1:25k topo	150	166	42	6.9	8
33	Llechwedd-y-Creigiog	Swansea	1	P	594617	5351046	594729	5351229	130	1:25k topo	130	176	32	6.8	20
34	Cherry Tree Hill	Swansea	1	P	594413	5352608	594525	5352791	175	1:25k topo	310	6	37	6.6	11
35	Lake Leake Rd P south	Swansea	1	P	579990	5347886	580102	5348069	270	1:25k topo	220	96	50	6.7	18
36	Lake Leake Rd P north	Swansea	1	P	577608	5347938	577720	5348121	360	1:25k topo	360	46	50	6.5	17

3: Table of beetle species/morphospecies sampled

-see attached Excel file

4: Table of spider species/morphospecies sampled

-see attached Excel file

Addendum:

- A list of references used for identification of Tasmanian beetles and spiders may be found by following this link: https://sites.google.com/site/lynneforster/taxonomyreferences
- Some background information on the relationship between beetles and fungi
- And
- Background information on the effect of pitfall trapping and different solutions in pitfall traps on the species sampled, may be found at the following link:

  https://sites.google.com/site/lynneforster/beetleecology