FIRE AND INVERTEBRATE CONSERVATION IN THE CENTRAL JARRAH FOREST OF SOUTH-WESTERN AUSTRALIA

FINAL REPORT

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ABSTRACT

A four year study of the effects of spring and autumn prescribed fires on surface-active litter invertebrates was carried out using pitfall trapping in Jarrah *Eucalyptus marginata* forest within the high rainfall zone of south-western Australia. Approximately 110,000 specimens were collected and identified to Order level for major groups and to family and morphospecies level for Coleoptera. Total morphospecies richness was also assessed for each sample throughout the study. Fire impacts on nine broad forest floor microhabitats were assessed by mapping their pre and post-fire extent. Regrowth of common understorey plant species and the build-up of leaf litter were monitored over the entire study period.

Mean sample richness of all higher taxa, at unburnt sites, was highest in spring with 89.8 morphospecies per sample and lowest in summer and autumn with 54.0 morphospecies per sample.

Litter depth, cover and volume recovered to pre-fire values within three years of both spring and autumn fires, while understorey shrubs showed a more rapid recovery after a high intensity autumn fire. Season of burning influenced microhabitat diversity, with high intensity autumn fire favouring the creation of ashbeds and moss swards which play a key role as microhabitats for invertebrates. Total abundances of litter invertebrates did not differ significantly between burnt and unburnt sites or between spring and autumn burns except during autumn periods, when abundances were up to 28% higher in the spring-burnt sites due to significant increases in Isopoda and Pauropoda. Season of burning also affects beetle species composition: of 149 beetle morphospecies trapped during the study period, 39 were trapped only at the spring-burnt sites, 18 were trapped only at the autumn-burnt sites and 29 were trapped only at the unburnt control sites. The remaining 63 beetle morphospecies were trapped at both burnt and unburnt sites.

Abundance of Araneae, Hemiptera, Orthoptera and Lepidoptera larvae declined significantly for up to two years, and Apocrita and Dermaptera for at least four years, following fire. Sample morphospecies richness of Araneae, Apocrita and Orthoptera declined significantly for at least two years on burnt sites, while that of Dermaptera, Pauropoda, Blattodea and Thysanoptera increased. These groups appear sensitive to fire and offer potential as bio-indicators of recovery.

Abundance of Coleoptera morphospecies immediately following the spring fires was almost four times that at unburnt sites. The biomass of Coleoptera morphospecies of the decomposer guild increased for at least two years following the fires. The large predatory guild had a biomass 18 times higher than unburnt sites, four years after the autumn fires. Site sample richness of Coleoptera morphospecies declined and species composition changed following spring and autumn fires, while regional bio-diversity increased. The study of fire impacts at the morphospecies level offers potential to link fire induced changes in ecosystem functions with changes in the biodiversity of litter invertebrate communities.

Results from this study suggest that a mosaic of long-unburnt, autumn-burnt and spring-burnt areas throughout the central jarrah forest should maximise habitat heterogeneity and the biodiversity of litter-dwelling invertebrates.

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SUMMARY AND RECOMMENDATIONS

A four year study of the effects of prescribed fire on litter invertebrates was carried out in jarrah *Eucalyptus marginata* forest in the high rainfall zone of south-western Australia. Changes in the abundance and richness of the surface active litter invertebrates were determined by pitfall trapping. Approximately 110,000 specimens were collected and identified to Order level for major groups and to family and morphospecies level for Coleoptera. The impact of the prescribed fires on nine broad forest floor microhabitats, which may act as refuges during fire for common and relictual invertebrates, was assessed by mapping their pre and post-fire area. Regrowth of the common understorey plant species and the build-up of leaf litter were monitored over the entire study period.

Overall invertebrate abundance and richness at long unburnt sites peaked in spring and was lowest in autumn. At these sites the nine most speciose orders contained approximately 90% of total sample richness, but community composition made small shifts from year to year. The rank sequence of the most speciose orders was seasonally cyclic and predictable, but sample richness and abundance within these orders underwent small unpredictable shifts reflecting year-to-year climatic influences. Changes in ordinal composition at the unburnt sites had returned to the initial composition by the end of the four year post-fire period, suggesting long unburnt composition may be cyclic or successional in the longer term. Over the four year study the rank sequence (in decreasing order) of the nine most speciose orders (or higher taxa) in spring was ants, wasps, beetles, spiders, flies, hemipterans, mites, collembolans and orthopterans. Effective monitoring of the small year-to-year (annual) shifts in richness and composition required the use of at least three (Araneae, Collembola and Thysanoptera) of these most speciose orders to distinguish them from the cyclic seasonal changes.

The season of burning had varying impacts on invertebrate composition. Following the autumn 1993 prescribed fire 31 orders were trapped, compared with 25 at the spring 1994 burnt sites and 24 at the unburnt controls. The greater order richness at the burnt sites was due to the capture of additional taxa from relict groups such as Mecoptera, Tricladida and Embioptera. Total invertebrate abundances did not differ significantly between spring and autumn burns except during autumn periods, when abundances were up to 28% higher in the spring-burnt sites due to the significant increases in Isopoda and Pauropoda. The season of burning also affected beetle species composition: of 149 beetle morphospecies trapped during the study period, 39 were trapped only at the spring burnt sites, 18 were trapped only at the autumn 1993 burnt sites and 29 were trapped only at the long unburnt control sites. The season of burning also resulted in differences in the magnitude and composition of beetle biomass at the post-fire sites. In November 1996, at least two years after the prescribed fires, the beetle biomass at the autumn 1993 burnt sites was approximately 13 times higher than that at the spring 1994 burnt sites and 18 times higher than that at the unburnt control sites. This result may appear to conflict with the lack of differences in post-fire invertebrate abundances, but indicates that the beetle biomass at the autumn 1993 burnt sites was largely partitioned into the higher trophic guild of large predatory beetle species (Carabidae). Beetle biomass at the spring 1994 sites showed that a greater proportion of biomass was made up of the lower trophic guilds of decomposers

(Tenebrionidae), herbivores (Scarabaeidae, Chrysomelidae and Curculionidae) and small predators (Staphylinidae). At the unburnt control sites in November 1996 the beetle biomass was largely partitioned amongst the trophic guilds of herbivores (Scarabaeidae and Curculionidae) and the small predators (Staphylinidae).

In the first two years after fire there were few significant differences in ordinal composition between the spring and autumn burnt sites, but there were marked differences between burnt and unburnt sites. In the first year after the prescribed fires significant declines occurred in the sample morphospecies richness of Araneae (spiders), Apocrita (wasps) and Orthoptera, and significant increases occurred in the sample richness of Thysanoptera. By three to four years after the autumn 1993 prescribed fires multivariate analyses indicated that the majority of higher taxa had returned to compositions similar to the unburnt sites. Significant reductions, however, still occurred in the sample morphospecies richnesses of Araneae and Apocrita, and significant increases in the richness of Dermaptera, Blattodea and Pauropoda. Lower sample species richnesses should be viewed with caution, however, as they may simply reflect a higher species turnover rate at the burnt sites, rather than a reduced total richness. In November 1996, two years post fire, the spring burnt sites had a lower beetle sample richness than unburnt sites, while the total post-fire beetle richness was slightly higher at the spring burnt sites with 88 beetle morphospecies trapped compared to 78 at the unburnt sites.

Lower intensity spring and autumn fires had little impact on the proportional area of the more restricted microhabitats of the nine broad forest floor microhabitats. The high intensity fires caused large reductions in the extent of log microhabitats, and an increase in the ashbed and moss sward microhabitats. In the longer term ashbeds are colonised by mosses to create moss swards, indicating that these higher intensity fires may play a key role in the long term maintenance of the diversity of jarrah forest floor refuge microhabitats.

Spring and autumn prescribed fires both caused an increase in the beetle biomass or beetle productivity of the litter invertebrate community at an early post-fire successional stage. The changed community composition, particularly of the spring-burnt sites, increased the richness of higher taxa and beetle morphospecies of the study area. The increase in productivity following the prescribed fires was first apparent in November 1994 with an increase in the abundance of small decomposers and small predators, such as the beetles (Hydrophilidae and Acanthocnemidae) and the collembolans. Early ramifications in November 1996 of this increased productivity became apparent further up the food web with the increased trophic level biomass of the large predatory beetle guild.

The results of this study indicate that spring and autumn prescribed fires in jarrah forest cause distinct impacts on litter invertebrate microhabitats, ordinal composition and beetle morphospecies composition and biomass. These results have implications for the management of fire in the central jarrah forest if the maintenance of biodiversity is to be achieved. In order to enhance the conservation of litter invertebrate communities, and ultimately higher order plants and animals, we propose the following guidelines for fire regimes in the central jarrah forest, with particular relevance to the upland ridge Dwellingup landforms:

(i) A mosaic of spring-burnt, high intensity autumn-burnt and longer unburnt areas should be maintained to provide habitat for a wide range of invertebrate groups, and to take account of relict and other taxa that favour or exclusively require certain environmental conditions. Patches of forest, maintained through burning in differing seasons, intensities, frequencies and at varying scales, should be interspersed in order to maximise the potential for cross-colonisation by all species, including those of low mobility.

(ii) The use of a variable prescription based on on-site habitat characteristics (such as microhabitat proportional areas not less than 5.0% for logs and not less than 0.2% for moss swards) and also the spelling of areas for a rotation every third or fourth cycle (Burrows pers. com.) should maximise the biodiversity of the litter fauna community in the central jarrah forest, including those elements which are uncommon or are particularly sensitive to fire. These latter populations may require further demarcation, protection and study of their habitat and life history requirements to determine locally appropriate fire regimes.

(iii) An unburnt period of at least four years between prescribed burning of forest areas and greater unburnt periods, to be determined by further research, for forest areas containing rare or relictual species particularly from the 29 morphospecies of beetles exclusively trapped from the long unburnt sites or from the Araneae and Apocrita taxa.

(iv) Further research is needed; a) to better delimit the relationship between refuge microhabitats (particularly logs and moss swards) and rare or relictual invertebrate species; and b) to investigate the further use of species composition and biomass of the common invertebrate guilds as bio-indicators of critical changes in ecosystem functioning and biodiversity and ; c) to compare long-term effects of different fire regimes; specifically to confirm that the recommendations (i) and (ii) continue to conserve the biodiversity of the litter invertebrates.

(v) It is desirable that future research on litter invertebrate ecology uses methods similar to those used in this and other recent studies (Friend and Williams 1997) to produce quantitatively comparable results, specifically with reference to pitfall trap dimensions, trapping preservatives and stratification of pitfall traps across microhabitats. Sampling dates should be temporally stratified to at least sample the annual peak in invertebrate sample richness and the annual low in sample richness and with a balance of pre and post-fire monitioring periods (Friend 1995).

INTRODUCTION

"...the very extraordinary devastation by fire which the vegetable productions had suffered throughout the whole country we had traversed....we did not see a spot...which had not visibly felt its effects. Where the country was well wooded the loftiest timbers had their topmost branches burned; yet none seemed totally destroyed..." (Capt. George Vancouver at King George Sound, south coast of Western Australia in 1791 (Vancouver 1801)).

Context

The dry sclerophyll forests of southern Australia are some of the most fire-prone ecosystems in the world. The role of regular prescribed burning in the conservation and management of these forests is a complex and sometimes contentious issue. The relative impacts of spring and autumn prescribed burning in the jarrah forest of Western Australia is a controversial issue. There is an ongoing need for objective, experimental research and feedback to enable correct management decisions to be made. Incorrect decisions have the potential to jeopardize the long-term survival of many species and ultimately, the maintenance of ecological processes in these forests.

This project addresses the role of fire in the maintenance of ecological processes in forests and uses empirical information on litter fauna invertebrates to examine fire management practices in relation to sustainable resource use.

Biogeographic setting

Climate and vegetation

Within the eucalypt forests of south-western Australia over the last 6,000 years there has been large alternations and distributional changes of the dominant eucalypt species (Churchill 1967) as a result of marked changes in climate and the frequency of fire. The climatic fluctuations have resulted in a more seasonally adapted biota in south-west Australia, with a high level of endemism (Kemp 1981, White 1990, Hopper et al. 1996). The persistence of the sclerophyllous vegetation and evidence of an increase in fire frequency in the recent past suggests that Aboriginal burning practices were a major factor in the persistence of the sclerophyll vegetation in Australia (Singh et al. 1979). The current climate of south western Australia, with cool wet winters followed by hot dry summers with frequent thunderstorms, has led to a particularly fire-prone environment with numerous lightning-ignited wildfires occurring annually (Collett *et al.* 1993, CALM 1994).

Recent fire history

In the jarrah forest of south west Australia fires were frequent and of low intensity prior to european settlement and subsequently changed to less frequent, intense fires following early agricultural development and timber harvesting. In 1918 a policy of fire exclusion was introduced, and maintained until 1954 when broadscale fuel reduction by prescribed fire was introduced. This current policy has been adapted since the 1970's to create favourable habitats for selected animal species (Christensen and Kimber 1975, Christensen 1983), to suppress dieback disease (Shea et al. 1981, Burrows 1985), to meet silvicultural requirements (Stoneman et al. 1989) or to protect fire exclusion areas (Christensen and Abbott 1989). An estimated 70% of the south west forests are subject to prescribed burning on a rotational basis, the length of time between fuel reduction burns based on the accumulation rates of fuels on the forest floor. In the jarrah forest the average time between fires prescribed for fuel reduction is 5 - 6 years (Wardell-Johnson and Nichols 1991). Nature Reserves and National Parks contain both areas of no planned burn and buffer areas prescribed burnt for wildfire suppression; a further 42 fire exclusion areas are protected from fire (Christensen and Abbott 1989).

Fire is a management tool which may be deployed to make broadscale ecological changes to the heterogeneous and diverse habitats of the south-west forests and woodlands. The impact of weather, fuel characteristics and other parameters on fire behaviour are relatively well understood (Burrows 1996). In contrast, research on the impact of fire on the biota, particularly invertebrate communities, of these south-west habitats has often produced conflicting conclusions, despite a number of studies (Christensen and Abbott 1989, Friend 1995, Friend and Williams 1996, Didham et al. 1996).

Invertebrates and fire

The majority of the biological diversity of ecosystems is contributed by invertebrates (IUCN 1983, Greenslade and Greenslade 1984, New 1984, CONCOM 1989), and they are now recognised as central to ecosystem functioning, yet are often ignored in ecological research. Certain groups of invertebrates are proving to be excellent bio-indicators of environmental conditions, and their study may contribute much to an understanding of the processes involved in pyric disturbance ecology.

South-west forest ecosystems contain an estimated 18,000 invertebrate species of which only an estimated 10% have been formally described (Abbott 1995). For most of the formally described species there is little or no life history or ecological information. The huge abundances and diversity of invertebrates has long been an obstacle to the comprehensive taxonomic and ecological study of invertebrate communities (New 1987). Added to these old problems is a growing awareness of the necessity of studing impacts on invertebrate communities at the individual species level (Friend and Williams 1996; Neumann and Tolhurst 1991). New (1984) emphasises that "species cannot be conserved without a habitat". CALM's Central Forest Regional Management Plan (1987-1997) states "A major aim of management in areas whose primary function is wildlife conservation is to maximise diversity and species richness. In some reserves, management is directed to providing habitat for particular species or communities."

Most studies have found a high degree of variability within and between sample sites. Campbell and Tanton (1981) in a comparison of fire impacts on the litter invertebrates in eucalypt and pine forests in the Australian Capital Territory, attributed this largely to small scale heterogenerity of the microenvironment within each sample site. Due to the large numbers of invertebrate individuals and species trapped on the jarrah forest floor, the majority of previous studies have only been able to assess the impacts of fire on invertebrate community composition at the order level. Litter invertebrate numbers appear to be highly variable in response to both changes in short-term climatic conditions and small scale spatial variation in their habitats (Campbell and Tanton 1981, Friend 1995). This makes the detection of fire impacts in short-term experimental studies, or by the use of space-for-time studies, problematic. To further confound the prediction of fire impacts on litter invertebrate communities, trapping techniques have varied from study to study, making quantitative comparisons impossible (Friend 1995).

Campbell and Tanton (1981) highlighted the importance of measuring fire impacts on the forest floor microhabitats and stressed the importance of refuge microhabitats, such as patches of unburnt litter and the large woody fraction, in litter invertebrate recolonisation of burnt sites. Fallen logs may be a particularly important refugium from harsh environmental conditions, such as fire or seasonal drought (Tanton and Campbell 1981). Fire damage to trees hastens the falling of large logs or branches to the forest floor and enhances their suitability as habitat by promoting hollow formation (Williams and Faunt 1997,Whitford and Williams 1997). Fallen logs are a limited and important fire refuge for vertebrates and a wide variety of invertebrates. Fire, therefore, plays an important role in enhancing the structural diversity of microhabitats and maintaining the balance between relatively common and more restricted refuge microhabitats, and in turn facilitates the maximisation of biodiversity of the litter invertebrates in the jarrah forest ecosystem.

A number of rare or relict invertebrate species in south west Australia are thought to be dependent on restricted forest floor microhabitats as refuges from fire and harsh environmental conditions. Several of the better studied species include the Midget spiders such as those from the family of Micropholcommatidae, which are thought to be dependent on the moss swards on the floor of the jarrah forest for breeding sites. Another is the Lungless spider (*Chasmocephalon* sp.) that constructs minute orb webs in the ends of fallen logs or burnt-out hollow butt trees in Tingle forest on the extreme south coast of Western Australia (Main 1987). Both these taxa illustrate the dependence of relict invertebrates on restricted microhabitats that may be created or destroyed by periodic fire, or act as refuges during these fires.

Most studies on the impact of fire on invertebrate communities have not measured the changes or return of habitat structure to pre-fire configurations (Yen 1987, Friend and Williams 1996). A small number of studies have identified invertebrate taxa that have specific habitat requirements in both undisturbed and post-disturbance plant communities. Michaels (1995) found a strong correlation between carabid beetle species and the structure of wet sclerophyll forest in Tasmania after logging, while Yen (1987) found that Coleoptera had specific habitat requirements in the undisturbed Victorian mallee communities. In south west Australia Main (1987) indicated that a number of relictual spider taxa required specific small scale microhabitats as both habitation sites in undisturbed forest and refuge sites during fire disturbance.

Previous research on the impact of fire on the litter invertebrate communities of the dry sclerophyll forests of southern Australia has often reported apparently conflicting results, possibly due to the examination of only a small section of the large spectrum of temporal and spatial variation (Abbott 1984, Majer 1985a, Friend and Williams 1996). Early studies on the jarrah forest litter invertebrates suggested that cool spring fires had a significant impact on the litter fauna for a period longer than 4 years (McNamara 1955, Springett 1976a). The majority of more recent studies suggested that most of the jarrah forest litter invertebrates (measured at the order level) recovered within 2-3 years. However, fire often has differential effects on different taxa, making predictions of impacts on community functioning difficult (Bornemissza 1969, Majer 1980, 1984, Abbott 1984, Abbott et al. 1984, Friend 1995).

Studies in dry sclerophyll forests of eastern Australia also broadly agreed on a 2-3 year recovery of litter invertebrate communities after prescribed fires (Campbell and Tanton 1981, Neumann and Tolhurst 1991, Collett et al. 1993). Collett and Neumann (1995) studied the impact of two spring fires, applied within three years of each other, on the activity of litter surface active Coleoptera. They found no long-term impacts on either the richness of all beetle species or the richness of 28 rarely trapped beetle families. They also assessed the impacts of these two fires on the beetle trophic guilds and found a short-term increase in the abundance of decomposer families. Few other Australian studies to date have attempted to link fire impact changes in litter invertebrate composition through trophic guilds or biomass production to the functioning of the litter invertebrate communities or the whole ecosystem in general.

In an effort to gain a greater understanding and predictability of environmental disturbances on the composition and functioning of Australian invertebrate communities, an increasing number of studies are attempting to relate the impact of disturbances on the taxonomic richness of selected bio-indicator taxa with the impacts on the whole community composition. Useful bio-indicator invertebrate groups identified to date include ants (Majer 1983, Andersen 1987), beetles (Michaels and McQuillan 1995, Lawrence and Britton 1991), wasps (New 1987), spiders (Main 1987, Friend 1995), Lepidoptera, Isopoda, Blattodea and Thysanura (Friend 1995). These studies suggest that a wide range of taxa containing a diverse variety of guilds are proving to be useful bio-indicators of both compositional and functional changes in some Australian ecosystems.

Objectives

This study was designed to determine guidelines for fire regimes that would both maximise the regional biodiversity of jarrah forest floor invertebrate communities and protect or enhance the less common invertebrates and their habitats. Lamont (1995) stated that biodiversity is the result of the interaction of three major components: composition, structure and function. To determine impacts on biodiversity it is necessary to determine the changes in species composition and structure (species biomass or species shape) on the ecosystem functioning (trophic biomass) (Hobbs 1992, Lamont 1995, Didham et al. 1996). The general aim of this study was therefore to determine the effects of prescribed fuel reduction fires on the biodiversity of litter invertebrates by (i) measuring changes in the abundance and composition of litter invertebrates at the ordinal level, and (ii) measuring changes, for Coleoptera, in their morphospecies composition and morphospecies biomass and associate these with changes in their trophic biomass.

The specific study aims were:

i) To examine the effects of routine spring and autumn fuel-reduction burning in jarrah forest in southwest Western Australia by studying components of the terrestrial invertebrate fauna that are both critical to ecosystem functioning and biodiversity and are likely to show a range of responses to fire; and

ii) In conjunction with other studies of vertebrates and vegetation in the same area, to develop general principles and policies for predictive fire management and the conservation and sustainable use of resources in such forest ecosystems.

MATERIALS AND METHODS

Study area

Soils and Landforms

The study was conducted in the Batalling and Nundedine Forest Blocks, 35 km east-north-east of Collie. The region has a distinctly mediterranean climate, characterised by hot dry summers and cool wet winters. This area extends through the central and eastern portions of the High Rainfall Zone of the South West Botanical Province (Hopper 1979, Beard 1980), in which the annual rainfall declines (1100 - 600mm) along an easterly gradient from the western edge of the jarrah forest. The central jarrah forest forms the large, central portion of the jarrah forest region in the Interim Biogeographic Regionalisation of Australia (Thackway and Cresswell 1995).

The 14 study sites were located on the Dwellingup soil and landform unit. The Dwellingup unit is the remnants of the ancient lateritic duricrust that caps the ridges of the gently undulating landscape of the Darling plateau, generally north of the Collie River and extending eastward from the Darling Scarp faultline. The ancient lateritic duricrust and profile has been eroded and dissected to form a complex network of swampy depressions and gently sloping minor valleys which usually drain in a north-westerly or south-easterly direction as a result of the grain of the underlaying Archean rocks (Briggs et al. 1980).

The tectonic stability, lack of recent glaciation, low relief and slow local erosion of these landforms has allowed the persistence of some of the early Tertiary landscapes. Upland remnants of Tertiary plateau surface still exist, even in the transitional rainfall zone where erosion was more active. The existence of these Tertiary landscape remnants and the persistence of relatively humid climatic conditions in the high rainfall zone has provided greater habitat continuity over a long period of geological time, thereby protecting many relict species from extinction (Hopper 1979).

Vegetation

The vegetation complexes of the Dwellingup soil unit of weathered lateritic remnants on the upland ridges in the study site have been defined as the Yalanbee and Dwellingup vegetation complex (Smith 1974, Churchward and McArthur 1980, Havel 1975a,b). This complex consists of a mixture of an open-forest of jarrah (*Eucalyptus marginata*)-marri (*Corymbia calophylla*) and a woodland of wandoo (*Eucalyptus wandoo*)-marri and is restricted to the 600 - 850 mm rainfall zone that contains the central and eastern edge of the jarrah forest.

Sampling Protocols

Experimental Design

Six sampling areas, each of about 1500 ha, with two replicate sampling sites within each, were established in either November 1992 or April 1994. Two additional sites were established in Fleays Forest Block south-west of Batalling in November 1992 in order to monitor the effects of a routine aerial burn scheduled for the following autumn. Each site was sampled up to four times each year, in spring, summer and autumn. During each of the final two years of the study in 1995 and 1996 two samples were taken, one each in spring and autumn. The two forest areas which were designated as "control" areas were unburnt since spring 1984, and comprised site 5 (500m west of spring 1994 burnt site 4), site 6 (600m east of autumn 1996 burnt site 7), site 9 (600m south of autumn 1996 burnt site 8) and site 10 (500m north of spring 1994 burnt site 12). The remaining five forest areas had been previously burnt in spring 1984, 1985 or 1988 and during this study were subjected to a range of prescribed fires: sites 1, 2, 7 and 8 were burnt in April 1996, sites 3, 4, 11 and 12 in September 1994, and sites 13 and 14 in April 1993.

Pitfall trapping of invertebrates

Invertebrates were sampled using pitfall traps, beginning in November 1992 at sites 13 & 14 and sites 3 & 11. These sites were sampled at least once per season between spring 1992 and autumn 1994, resulting in 6 sample periods up to April 1994. In April 1994 sampling began at all sites and continued at least once per season until the completion of the study in March 1997.

Each sampling site comprised a 15 x 15m grid of 16 pitfall traps in a 4x4 array, at 5m spacing. The 4 pitfall rows of each grid where aligned parallel to the slope contours at each site. Each pitfall trap was a plastic cup 90 mm in diameter and 110 mm deep, placed inside a sleeve of PVC piping to minimise disturbance to the soil and litter during setting. The diameter of these cups was chosen to be larger than the largest invertebrate species that were expected to be collected during this study (i.e. orthopterans, carabid beetles and mygalomorph spiders). This avoided any possible sampling bias that may occur when pitfall traps with smaller diameters are used.

During the sampling period, traps were opened and three-quarter filled with Galt's solution (5% sodium chloride, 1% potassium nitrate, 1% chloral hydrate, a trace of glycerine and 93% water) (Friend and Williams 1996). Traps were opened for 10 days to reduce possible sampling bias due to short term weather fluctuations, as well as to increase the number of invertebrates captured (Fig. 2). At the end of each sampling period the four traps at each corner of the grid were bulked to give four samples per grid. The samples were fine sieved (0.2 mm x 0.2 mm mesh size) and transferred to a solution of 70% ethanol for transportation to the laboratory. Trapping cups were then removed from the PVC tubes and replaced with cups filled with undisturbed soil and surface litter to close the traps between sampling periods.

Figure 2. An operational pitfall trap, three-quarters filled with Galt's solution. The non-trapping period soil cup has been removed and can be seen on the left.

Sorting of invertebrates

Invertebrate samples were sorted using a binocular microscope, usually using the 6.5 x 10 objectives. All macro and meso-invertebrate specimens (those greater than 0.2 mm body dimensions) were identified and separated to order level using the keys of Harvey and Yen (1989). For each invertebrate order the number of individuals and the number of different morphospecies were counted within each sample to estimate sample richness.

Beetles were identified to morphospecies using the methods of Oliver and Beattie (1992). Both adult and larval beetle morphospecies were distinguished and compared to the beetle reference collection to estimate total beetle richness at each site and between all sites within the study area. Beetle morphospecies were assigned a species code and the number of individuals of each was counted. Each morphospecies was further identified to family level using the keys of Lawrence and Britton (1991). The biomass of each beetle morphospecies was estimated by measuring body length (anterior clypeus margin to abdomen tip), body width (anterior margins of elytra) and body depth (dorsal anterior elytra to ventral metasternum), to the nearest 0.1 mm. Biomass as volume in cubic millimetres (cu. mm.) was calculated as the product of these three measures. Volume is a more relevant measure of biomass than weight in trophic guild studies (Pianka 1986, Chapt. 4).

Oliver and Beattie (1992, 1996) have shown that surveys of beetle morphospecies have strong concordances with conventional beetle species surveys and demonstrated that morphospecies inventories are a rapid cost-effective method of determining both richness (alpha-diversity) and turnover (beta-diversity) of select invertebrate taxa (particularly ants and beetles) in assessments of changes in surface-active invertebrate biodiversity.

Habitat Structure

Forest structure and habitat parameters that may be of relevance to terrestrial invertebrates were quantified at each site. Vegetation structure, defined as the modal maximum height and density of common understorey plants species less than 2 m in height, was estimated for the whole 15m x 15m grid at each site at 2 monthly intervals.

Leaf litter depth was measured at a point 30cm from each of the 16 pitfall traps at each site and mean litter depth calculated from the 16 litter depth points at each site. Leaf litter cover was estimated in a 30cm x 30cm area adjacent to each of the pitfall traps, with cover scored as 0 = absent, 1 = 1-25%, 2 = 26-50%, 3 = 51-99% and 4 = 100% (Friend and Williams, 1996).

Common forest floor microhabitats were mapped to determine their areal extent, their potential as fire refugia, and to determine the role of fire in modifying their relative extent. These microhabitats consisted of nine non-living physical structures that could be used as refuges during fire: bare soil, unburnt litter, burnt litter, rocks (>50 mm diameter), logs & branches, log ashbeds, dead stumps, burnt-out stump holes, and termite mounds. A further nine microhabitats were selected to focus specifically on the extent and survival of moss (*Funaria hydrogrammetrica*) swards in each of the nine forest floor microhabitats. Areas of each microhabitat were mapped within the 225 sq.m. of each site at approximately 2 monthly intervals.

Prescribed fires

Sites 13 and 14 unburnt since spring 1985 were subjected to an autumn prescribed fire in April 1993 under dry weather, dry soil and dry fuel conditions. The resulting fires were of high intensity at site 13 with total crown scorch to 25 m. (estimated Byram's fire intensity 1000 - 1200 kW/m, Burrows 1997) and medium intensity at site 14 with patchy crown scorch to 25m (600 - 1200 kW/m). Two forest areas, unburnt since spring 1984, containing sites 3, 4, 11 and 12 were spring burnt in September 1994. The intensity of burn at each forest area was different: at sites 3 & 4 the fire was of low intensity with leaf scorch generally not exceeding 1.5m above ground (estimated intensity less than 100 kW/m); at sites 11 & 12 the fire was of moderate to high intensity, with crown scorch ranging from 6 to 25 m above ground (estimated intensity 250 - 1200 kW/m). A similar situation occurred in the two areas burnt in autumn 1996. Sites 1 & 2 were aircraft ignited (incendiary spacing 200 x 200 m.) on the evening of the 29 April 1996 and burnt at very low intensity inward (soil moisture content 12%, flame height 0.4 m., rate of spread 20m/hr., < 100 kW/m.) from the block boundaries and across the experimental sites overnight; the following day the core of the area continued to burn at a much higher intensity. The overall result was that the area had a mosaic of burnt patches of different fire intensities. On the same day (30 April 1996) sites 7 & 8 were ignited, during mid-morning. This fire burnt throughout the day, again resulting in a diversity of fire intensities (soil moisture content 9%, flame height 0.4 to 1.0 m, rate of spread 26 m/hr., < 200 kW/m.) with some portions (including site 8) burning at a high intensity (< 1200 kW/m.), with complete crown scorch to 25m and subsequent leaf drop and seed release (Van Heurck, personal observation).

Statistical Analysis

The impact of fire on the abundance and composition of the jarrah forest litter invertebrate community was analysed using the Before and After Control-Impact (BACI) method of analysis (Stewart-Oaten *et al.* 1986, Underwood 1991). This approach treats the replicate samples (over time) within each study site as true replicates, in order to assess differences between fire treatments. Spring and autumn samples were analysed separately because there were a large number of effects contributing to the variation in each sample (viz. year-to-year, number of years post fire, area, season-of-burn and season-of-sample effects). Preliminary analyses indicated that the spring versus autumn differences were the largest source of variation and hence the most likely to obscure more subtle changes due to the other effects. Thus by removing the sample season effect, we sought to increase the sensitivity of the analysis to fire impact and other effects. Data were appropriately transformed in order to achieve homoscedasticity and approximate normality of residuals: abundance data were logarithmically transformed whereas richness data did not require transformation.

Two major aspects of the effects of fire were examined. First, post-fire changes in the abundance and species richness of invertebrate orders were analysed for both spring and autumn samples at all sites after fire. To determine the statistical significance and magnitude of any post-fire impacts, changes after fire were compared to the control sites for each of the following post-fire periods: (i) "early acute" phase- less than one year post-fire; (ii) "acute" phase- less than two years post-fire; (iii) "chronic" phase- between two to four years post-fire; and (iv) complete post-fire phase- up to and including four years post-fire. Second, post-fire changes due to the season of burn on the abundance and richness were analysed using the BACI model. Invertebrate order abundance and richness data for spring and autumn pre- and post-fire samples were compared to the control sites, and autumn-burnt sites were compared to spring-burnt sites to determine any fire impacts.

Pre- to post-fire changes in the composition of the leaf-litter invertebrate community were also examined using multivariate methods. The method of principal component (PC) biplots (Digby and Kempton 1987) was used: this provides a graphical display of changes in community structure (Williams 1994). The PC biplot is a simultaneous ordination of environments and taxa, and is interpreted by determining where each environment appears with respect to the axis of each taxon: in this case each "environment" was the sample taken at one area at one time, reduced to include only spring and autumn samples, and each taxon was an invertebrate order.

The method consists of the following steps: abundances were logarithmically transformed, and the sample by taxon matrix "double centred" so that each row and column had mean zero. These two steps reduce the dominance of the most abundant taxa and so emphasize relative rather than absolute changes in abundances (Digby and Kempton 1987). This matrix was subjected to principal component analysis using the covariance matrix, and the number of axes retained was determined subjectively by examining the scree plot of the variance explained by each component. Typically, six components were retained, each of which explained more than 5% of variance.

PC biplots are an effective method of graphically summarizing an environment by taxon matrix. Only the most dominant taxa, as determined by the magnitude of their associated eigenvector, were included on the biplot. In order to determine which axes to display in each PC biplot, we subjected the principal component scores to multivariate ANOVA, fitting effects for area, year and whether the sample was from a burnt or unburnt site. Principal component scores are by definition multivariate normal, and so satisfy the assumptions underlying MANOVA.

RESULTS

Habitat Structure

Litter

By March of 1996 both the sites burnt in autumn 1993 and those burnt in spring 1994 had accumulated a standing crop of leaf litter approximately 20 mm deep, similar to that of the unburnt sites (Fig. 3). This represented a recovery to pre-fire litter depth at the spring burnt sites after 16 months, and a recovery at the autumn 1993 burnt sites after 36 months. Analysis of the change in leaf litter depth over the 4-year post-fire period showed that the reduction in leaf litter depth at burnt sites was less than 8% ($p = 0.39, >0.05$) for the first two years, then recovered to became 20% ($p = 0.16, >0.05$) deeper than the controls during the third and fourth years following the fires (Table 1). Litter cover varied more substantially (Fig. 4). In the first two years after the fires there was a significant reduction in leaf litter cover of approximately 30% ($p = 0.006, <0.05$**) relative to unburnt sites and continued to remained below 15% ($p = 0.35, >0.05$) of the level in unburnt sites in the third and fourth years post-fire (Table 1).

Vegetation structure

Post-fire recovery of the vegetation structure was assessed by summing the modal top heights of the 19 most common understorey plant species for each sampling date at each site (Fig. 5). All 19 species were observed to have resprouted and grown new aerial shoots after the prescribed fires. In August 1994, approximately 1.5 years after the autumn 1993 prescribed fire, the mean modal top height of the understorey shrubs at these sites was 80.2% of that at unburnt sites. Also in November 1995, one year after the spring 1994 fires, the mean modal top height of understorey shrubs was 49.7% of the values in unburnt sites. In March 1997, four years post-fire, at the autumn 1993 burnt sites the mean modal top height of understorey shrubs was 14.1% greater than that of the control sites. The mean understorey height at this date, 28 months after the spring 1994 burns, was 65.7% of the control height (Fig. 5). The rate of regrowth of the individual understorey shrubs mirrored that of the pooled top height, with more rapid regrowth at the autumn 1993 burnt sites compared with the spring 1994 burnt sites (results not shown). At all burnt sites the same species exhibited the most rapid regrowth (eg. cycad *Macrozamia reidlei)*, reaching heights comparable to unburnt sites within a very short period, and typically exceeding these within 17 months post-fire (see Fig. 6,7&8).

Fig.6 Photo: Unburnt site (site 5), in March 1995 (Note the height of the cycad *Macrozamia reidlei,* centre).

Fig.7 Photo: Site 4 (adjacent to site 5), low intensity burnt in September 1994. This photo was taken in March 1995, 6 months after fire, and shows the rapid recovery of both leaf litter and shrub-layer species such as *Macrozamia reidlei*(foreground centre), *Persoonia longifolia* (foreground left) and jarrah saplings (behind *P.longifolia,* centre left).

Fig.8 Photo: Site 13, high intensity burnt in April 93. This photo was taken in March 1995, 23 months after fire, and shows the rapid recovery of shrub-layer species such as *Macrozamia reidlei* (right mid-ground), *Bossiaea ornata* (centre mid-ground) and numerous jarrah saplings.

Microhabitats

The relative availability of forest floor microhabitats, based on their range of percentage areas across all sites in the control and pre-fire sites, produced the following ranking of availability: unburnt leaf litter (84% - 96%), bare soil (0% - 10%), fallen logs and branches (0.5% - 5.1%), all moss microhabitats (0.1% - 1.2%), ashbeds (0.0% - 1.2%), dead stumps (0.03% - 0.4%), stump holes (0.0% - 0.2%), termite mounds (0.0% - 0.07%) and exposed lateritic rock surfaces (0.0% - 0.07%) (Table 2). The impacts of the season and intensity of the prescribed fires on microhabitat area were assessed using analysis of variance and single degree-of-freedom contrasts: the only significant changes were those to be expected in the abundance of the two types of litter (Table 2, Fig.9), although the high intensity autumn 1996 fire substantially reduced the log and branch microhabitat (5.11% to 2.74%), with a corresponding increase in ashbed (0% to 2.44%) (Fig.11). As stated above the extent of unburnt litter was significantly reduced by all fires. However the greatest reduction in unburnt litter was to 10.03% post-fire, at the low intensity autumn 96 burnt sites, which indicates that large patches of unburnt litter survived these fires (Fig.10).

Fig.9 Photo: Site 8 several weeks after the high intensity autumn fire of April 96. This photo shows a small patch of unburnt bare soil at the base of a jarrah (*E. marginata*) trunk on which a moss sward survived the high intensity fire.

Fig.10 Photo: Site 1 burnt under low intensity in autumn (April) 1996. This photo was taken several weeks after the prescribed fire and shows the large patches of unburnt leaf litter remaining after this fire, often on the upwind side of large logs.

Fig.11 Photo: Site 8 high intensity autumn burnt in April 96. This photo was taken several weeks after the prescribed fire and shows a smouldering fallen dead tree.

Invertebrates

Changes in abundance

The total abundance of invertebrates in the four spring samples following the prescribed fires was almost 40% below that found in the unburnt sites, although this decline was not statistically significant (Table 3). By contrast, the three autumn samples after the prescribed fires yielded 5% more individuals than the control sites, but again this was not a significant difference. Thus in the early acute phase the total abundances of invertebrates in spring were lower than those in the unburnt control areas, whereas the autumn abundances were higher. During the post-fire chronic phase (2-4 years) total abundances were reduced in both the spring and autumn seasons; however, none of these changes were sufficiently large to be statistically significant.

Total abundances represent the combined abundances of more than 20 litter invertebrate orders, each of which displayed differing responses to the prescribed fires. The statistically significant responses can be divided into three groups: (i) chronically reduced taxa, those having significantly reduced abundances in both the acute and chronic phases; (ii) acutely reduced taxa, with significantly reduced abundances in the acute phase but with abundances equal to or higher than control sites in the chronic phase; and (iii) increased taxa, with significantly higher abundances in either the acute or chronic phases.

Within the chronically reduced group were the, pollinating, predatory and herbivorous taxa, wasps (Apocrita $p< 0.05$), earwigs (Dermaptera $p< 0.05$) and Hemiptera ($p< 0.1$), all in spring (Table 3). Within the acutely reduced group were the, decomposer, herbivorous and predatory taxa, the mites (Acarina $p< 0.1$) and Lepidopterans ($p<$

0.05) which were reduced in the spring samples of the acute phase, the spiders (Araneae $p < 0.05$, $p < 0.1$) and crickets (Orthoptera $p < 0.05$, $p < 0.1$) which were reduced in both spring and autumn of the acute phase and the flies (Diptera $p < 0.1$) which were reduced in only autumn of this phase. All these taxa had returned to a level comparable to or higher than the unburnt sites by the chronic phase. The increased taxa comprised small decomposer and herbivorous taxa such as thrips (Thysanoptera $p < 0.05$), silverfish (Thysanura $p < 0.05$), slaters (Isopoda $p < 0.1$), termites ($p < 0.1$) and the seed-feeding or scavenging ants (Formicidae $p < 0.1$) in spring samples and, the decomposer taxa, psocids (Pscoptera $p < 0.05$) in autumn samples, all of which were substantially more abundant during the acute phase.

The impacts of season of burning on the post-fire total abundance of invertebrates of the spring prescribed fire was not distinguishable from the impacts of the autumn prescribed fires (Table 4). However, in the three post-fire autumn samples the total abundance at the spring burnt sites was 28% higher than the autumn burnt sites, at a level closely approaching significance ($p = 0.069$). The abundance of the small decomposing taxa Isopoda ($p < 0.05$) and Pauropoda ($p < 0.05$) was also significantly higher at the spring burnt sites during these post-fire autumns. The autumn burns appear to favour the scavenging or seed-feeding ants and the large saprophagous Blattodea (cockroaches) in the autumn samples.

Ordination of invertebrate abundance in spring by time since fire generally separated the unburnt and burnt sites into two groups (Fig. 12). Burnt sites typically had higher relative abundances of Thysanoptera and Blattodea, and lower abundances of Araneae, Lepidoptera and Hymenoptera (wasps only), and varied considerably in their abundances of Coleoptera, Diptera and Acarina for the first two years after fire. Unburnt sites had similarly high variation in the abundances of these three taxa. By three to four years after fire, invertebrate abundances on most burnt sites were similar to the unburnt sites. The four-year-old autumn 1993 burnt sites, for example, were more similar to the unburnt sites than to the younger burnt sites, apparently because of high abundances of Araneae, Lepidoptera and wasps. This analysis highlighted the potential of Araneae, Apocrita, Lepidoptera, Thysanoptera and Blattodea to indicate fire effects on spring abundances. However, there was no clear separation of spring and autumn burnt sites and ,also, there was no analysis of year-to-year effects using this method, based on time since fire of spring abundances.

Alternatively, ordination of spring abundances by year of sample had the potential to separate year-to-year effects from fire effects. This method of analysis, although clearly emphasising the influence of annual effects, only separated a few fire effects (Fig. 14). Unburnt sites sampled in 1992 and 1993 had relatively high abundances of Isoptera, and low abundances of Collembola and Araneae. In 1994 the unburnt sites had higher abundances of Araneae and Orthoptera, while the spring 1994 burnt sites had an intermediate abundance of all five taxa. In 1995 both burnt and unburnt sites had higher abundances of Collembola. In 1996 the unburnt controls had returned to a composition similar to that of 1992 and 1993. The majority of burnt sites, however, only partly followed this pattern and showed two widely diverged groups within each burn treatment. Some were indistinguishable from the control sites, whereas others had a marked increase in the abundance of Lepidoptera. The only fire effects to be clearly highlighted by this method of analysis were a decline in the spring abundance of Orthoptera and Araneae in spring 1994 (acute stage) and a increase at some burnt sites of Isoptera and Lepidoptera in spring 1996 (chronic stage).

Ordination of the autumn abundances by sample year only partly separated burnt and unburnt samples by fire effects (Fig. 13). All sites showed clear annual changes in relative composition. In 1993 all sites were unburnt and showed intermediate abundances of all the five major taxa depicted in the biplot. In 1994 the unburnt sites showed a high abundance of Orthoptera and low abundance of Acarina and ants, whereas the increase in Orthoptera was not found in the autumn 1993 burnt sites. In 1995 the unburnt group of sites had a reduced abundance of Orthoptera and Collembola, and an increased abundance of Coleoptera; the burnt sites were distinguished by a higher abundance of ants and Coleoptera and a reduction in Orthoptera. In 1996 the group of unburnt sites again showed a marked shift in composition, having a higher abundance of Collembola and reduced abundance of Coleoptera, and the burnt and unburnt sites became similar.

Some common trends emerged between the univariate and multivariate analyses. These were (i) a reduction in spring abundance of Apocrita during the chronic phase at burnt sites (Fig. 12, Table 3); (ii) a reduction in spring or autumn abundance of Araneae, Orthoptera and Lepidoptera during the acute phase at the burnt sites (Fig. 14, Table 3); (iii) increased abundances of Formicidae during the acute phase (Fig. 13, Table 3); and (iv) increased spring or autumn abundance of Thysanoptera, Blattodea and Isoptera during the chronic phase at burnt sites (Figs. 12, 14, Table 3).

Changes in richness

The average total richness of invertebrates in the four spring samples following the prescribed fires was 26% below that found in unburnt sites, although this decline was not statistically significant (Table 5). The three autumn samples after the prescribed fires yielded 6% higher average richness, but again this was not a statistically significantly difference. In the early acute phase the average total richness was lower in both spring and autumn. In the chronic phase there was a 31% reduction in spring average richness but a 24% increase in autumn richness relative to the unburnt sites; however, none of these changes were statistically significant.

Total average richness represents the combination of more than 20 invertebrate orders, each of which displayed differing responses to the prescribed fires. The observed responses were divided into three response groups: (i) chronically reduced taxa, those having reduced sample richnesses in both the acute and chronic phases; (ii) chronically increased taxa, with higher sample richness in the chronic phase or both; and (iii) acutely reduced taxa, with reduced sample richness in the acute phase but with richness equal to or higher than control sites in the chronic phase.

The chronically reduced group comprised spiders (Araneae $p < 0.05$) and wasps (Apocrita $p < 0.05$), both of which declined in spring samples (Table 5). Within the chronically increased group were earwigs (Dermaptera $p < 0.05$) and Pauropods ($p < 0.1$) in autumn, and cockroaches (Blattodea $p < 0.1$) and thrips (Thysanoptera $p < 0.05$) in spring. The acutely reduced taxa consisted of mites (Acarina $p < 0.1$) and Lepidoptera ($p < 0.1$) in spring and the orthopterans ($p < 0.05$) in autumn samples.

A total of 31 higher taxa were captured after the autumn 1993 fire, compared with 24 taxa at the unburnt sites and 25 taxa at the spring 1994 burnt sites during the same period (Table 6). The additional taxa were Tricladida (flatworms), Embioptera (web spinners), Mecoptera (scorpion-flies) and Polyxenida (millipedes). Taxa that were captured before the spring 1994 prescribed fires, but not after, were Gastropoda (snails), Symphyla, Oligochaeta (earthworms) and Tricladida.

The seasonal sample richness of invertebrates for the unburnt sites was assessed for the period May 1993 to November 1995, to determine any influence of seasonal factors on fire impacts. Data from this period suggested that the total richness in spring samples was markedly higher than the summer, autumn and winter samples (Table 7). The most speciose taxa were ants in spring samples, and wasps in autumn. In both spring and autumn samples the nine most speciose taxa together made up more than 90% of the total richness.

The ordination of average richness in spring shows a marked influence of year-to-year effects (Fig. 15). Both burnt and unburnt sites sampled in spring 1994 had higher average richness of mites (Acarina), spiders (Araneae) and wasps (Hymenoptera). In 1995 all sites had higher average richness of thrips (Thysanoptera), but this was less pronounced on burnt sites. In 1996 all sites had distinctly higher average richness of Orthoptera and Collembola, although the sites recently burnt (in autumn 1996) were atypical more rich in Collembola and Thysanoptera species.

The ordination of average richness in autumn distinguished both year-to-year and fire effects (Fig. 16). In 1994 all unburnt sites grouped closely together with a composition characterised by high average richness of Araneae and Diptera which was higher than burnt sites. In autumn 1995 the unburnt sites had a reduced richness of Araneae and a much higher richness of ants, while the recently burnt sites had a marked increase in ant richness. In autumn 1996 the unburnt sites shifted to a composition richer in Blattodea, Thysanoptera and Collembola, as did the burnt sites.

Some common trends emerged between the univariate and multivariate analyses. Two fire effects in common were (i) a acute reduction in autumn richness of Araneae at burnt sites (Fig. 16, Table 5); and (ii) a chronic increase in spring richness of Thysanoptera at the burnt sites (Fig. 15, Table 5). The multivariate analyses also detected two fire effects that did not reach significance in the univariate analyses. These were (i) a increase in ant richness in autumn 1995 at the burnt sites (Fig. 16); and (ii) a increase in Collembola richness in spring 1996 at the burnt sites (Fig. 15). The multivariate analyses were most useful in highlighting year-to-year shifts in the richness of taxa at the unburnt sites. Taxa that characterised unburnt sites with a increase in richness in a particular year, also, in the same year, showed a significant fire effect (higher or lower at burnt sites) in the univariate analyses. These taxa were Araneae, Apocrita, Acarina, Blattodea and Thysanoptera.

Changes in richness of beetle morphospecies

Over the entire study period a total of 149 morphospecies were found from 33 beetle families (Table 8). Total sample richness in November 1994 was 38% higher two months after the spring 1994 prescribed fires than at the unburnt control sites (Table 8). In November 1996, in the third spring following the spring prescribed fire, the total sample richness had declined to be 32% lower than that of the unburnt sites. The total sample richness of beetle morphospecies at the autumn 1993 burnt sites, in the fourth post-fire spring, was 49 % lower than the unburnt sites.

The most speciose trophic guilds collected, at all sites, were small predatory beetles of families such as the Staphylinidae and Pselaphidae, followed by herbivores (Chrysomelidae and Curculionidae) and decomposers (Mycteridae and Nitidulidae). During the post-fire period 63 morphospecies were recorded in both burnt and unburnt sites, 29 only at the unburnt, 18 only at the autumn 1993 burnt sites and 39 only at the spring 1994 burnt sites (Table 11). At the spring 1994 burnt sites the 32% reduction in sample richness in November 1996, and the higher post-fire total richness of 88 morphospecies, compared to 78 at the unburnt sites, indicate that species turnover was far more rapid at the spring burnt sites. Of the 39 beetle morphospecies trapped only at the spring burnt sites, the most speciose families were Carabidae, Curculionidae and Staphylinidae; the high dispersal ability of these families may explain the high species turnover at the spring burnt sites. The most speciose family at the autumn burnt sites was the Chrysomelidae. At the unburnt sites the most speciose family was the herbivorous Curculionidae.

Changes in abundance of beetle morphospecies

In November 1994, the total sample abundance of beetle morphospecies at the spring 1994 burnt sites was approximately four times higher than at the unburnt sites (Table 9). This was due to high abundances of Hydrophilidae and Acanthocnemidae: in November 1994 the sample abundance of Acanthocnemidae at the spring burnt sites was approximately 50 times that at the unburnt sites; at the autumn 1993 burnt sites was approximately 18 times higher (Table 9). By November 1996 the total sample abundance at the spring burnt sites had declined to approximately 50% of the control abundances and Acanthocnemid sample abundances had declined to closely approximate those at unburnt sites. At the autumn 1993 burnt sites in November 1996 the total sample abundances in this fourth post-fire spring approximated that at the unburnt sites, as did the sample abundances of Acanthocnemids.

Changes in biomass of beetles

Beetle biomass was markedly higher by November 1996 at the burnt sites. At spring burnt sites in the third year post-fire, the total mean volume of beetle morphospecies in spring was 42% higher than that at the unburnt controls (Table 10). This biomass was composed largely of the decomposer guild (mainly Tenebrionidae) and the herbivore (Chrysomelidae and Scarabaeidae) and small predator guilds (Staphylinidae). At the autumn 1993 burnt sites in the fourth spring the total mean volume of beetles was approximately 18 times that at the control sites and 13 times that at the spring burnt sites. This biomass was composed largely of the predatory higher trophic guild (Carabidae). At the unburnt sites in November 1996 the majority of the beetle biomass was partitioned almost equally amongst the herbivores (Curculionidae and Scarabaeidae) and small predators (Staphylinidae).

DISCUSSION

In a recent comprehensive review of ecological factors determining the biodiversity of ecosystems, Lamont (1995) points out that from a conservation point of view the question we wish to resolve is "how to optimise ecosystem functioning to maximise biodiversity?". He emphasizes that biodiversity can be divided into the three components, composition, structure and function, and suggests that monitoring the effects of experimental manipulation of two of these components (composition and structure) on the third (ecosystem function) would highlight the role of these major components in maximising the biodiversity of a ecosystem.

The overall objective of this study was to determine the role of spring and autumn prescribed fires on maximising the biodiversity of the forest floor litter invertebrate communities in jarrah forest of south western Australia. This study by monitoring the impacts of these prescribed fires on a number of parameters of the two components, composition and structure, of the jarrah forest floor litter invertebrate communities and their habitats, was able to highlight several important trends in the resulting community functions and community biodiversity. Each of these trends is discussed in greater detail below.

Habitat Structure

Litter

The recovery of leaf litter depth and cover to unburnt levels within three years following both the spring and autumn prescribed fires indicates that the structural and habitat complexity of the leaf litter layer also approximated that at the unburnt sites within three years of these fires. A number of previous studies have reported that the major factor limiting litter invertebrate abundance and richness is the amount of accumulated litter (McNamara 1955, Bornemissza 1969, Gill 1969, Uetz 1975 & 1979 and Majer et al 1997). While Campbell and Tanton (1981) reported that monitoring the spatial variability and structure of litter remaining after forest fires was critical to the interpretation of post-fire recovery of invertebrate communities. Majer (1984) reported that 13 months after a low intensity autumn fire in the jarrah forest the litter biomass had built up to 66% of the unburnt plot. The results of our study showed that the biomass of the leaf litter layer which accumulated over the three year post-fire period at the burnt sites was approximately 15,000 cc m^{-2}, well within the range of the litter biomass at the unburnt sites. The similar biomass of the standing crop of leaf litter at both burnt and unburnt sites indicates that litter decomposing invertebrate populations could attain similar biomass and abundances by the end of the three year post-fire period. Therefore the availability of litter three years after the fires is not likely to be a limiting factor in the functional process of biomass accumulation (and the resultant partitioning into total abundance) of the invertebrate community of the burnt sites.

The season of burning, however, resulted in a different rate of litter accumulation with a more rapid recovery of the leaf litter standing crop at spring burnt sites. This difference in rate of return to pre-fire litter volumes may have been due to two factors: first, prescribed burning in spring under wetter soil moisture conditions may reduce combustion losses of the highly decomposed litter or humus layer, and therefore reduce the initial loss of litter depth (Burrows, 1996); and/or second, the large increase in the abundance and biomass of litter decomposing beetles in spring of 1994 and 1995, and of Collembola following the prescribed fire at the sites burnt in autumn 1993, may have increased in the decomposition rate of the accumulating litter, which would have reduced the build-up of this litter. All burnt sites had recovered to be within the range of pre-fire litter covers within three years of the prescribed fires, and leaf litter depth had recovered by one and a half and three years. The impacts of the season of burn on the litter volume were no longer apparent after three years and therefore litter volume at these sites would not limit the function of invertebrate biomass accumulation in the long term.

Vegetation structure

Immediately after the passing of a fire the vegetation structure is simplified, following the destruction of most of the above-ground parts of the understorey vegetation. In burnt patches the majority of large vertical structures remaining were either unburnt portions of logs or live tree stems. Structural complexity at the burnt sites increased as the vegetation regrew to a height that approximated that at the unburnt sites. The unchanged floristic composition following the fires conforms to the 'Initial Floristic Composition Model' of post-fire succession shown by many Australian sclerophyllous vegetation types (Purdie and Slayter 1976). This unchanging post-fire plant species composition stressed the possible successional importance of the predictable post-fire change in the vegetation structure. The long unburnt sites may represent a climax vegetation structure of these post-fire structural changes.

The rate of regrowth and recovery of the understorey vegetation appears to have been affected by the season of burning. Three years after the fires the vegetation at the autumn 1993 burnt sites was 14.1% taller than at the control sites while the understorey vegetation at the spring 1994 burnt sites was 24.3% shorter two and a half years after fire. At all burnt sites the old senescent phenol rich foliage was replaced with a flush of rapidly growing, nutrient-rich foliage which may have favoured herbivorous and sap feeding invertebrates. The differing burning seasons appeared to have resulted in different rates of structural change in the vegetation which in addition to the vegetation structure of the long unburnt sites resulted in a greater structural diversity of the entire study area.

Yen and Butcher (1997) in their overview of the conservation of non-marine Australian invertebrates make the inference that, under the current state of incomplete knowledge, the use of large scale plant communities as the basis for conservation decisions is the most rapid way of adequately conserving most invertebrate taxa. Another recent review of insect conservation by Usher and Jefferson (1991) pointed out that a number of distinctive invertebrate communities were associated with particular successional stages of plant associations and active management of these successions was required to prevent the local extinction of invertebrate species within these communities. Danks (1979) in a review of the terrestrial habitats of Canadian forest insects concluded that local patches of disturbance are clearly important to maintain the diversity of the regional invertebrate fauna. Within the area of this current study the differing structural development of the vegetation at the burnt and unburnt forest areas would have provided a greater diversity of forest habitats to be colonised by the forest floor invertebrate fauna.

Microhabitats

Some of the more common apterous invertebrates that have low dispersal power, such as silverfish (Thysanura) and woodlice (Isopoda) survived the prescribed fires in high numbers. These taxa may have survived by using logs and other microhabitats as refuges from the spring fire. During the autumn 1996 fires one of us (PVH) observed invertebrates using both the cracks in logs and leaf litter beneath them as shelter. Campbell and Tanton (1981) made similar findings in a comparison of fire impacts on the litter invertebrates in eucalypt and pine forests in the Australian Capital Territory. They highlighted the importance of measuring fire impacts on the forest floor microhabitats such as patches of unburnt litter and the large woody fraction. They put particular emphasis on the possible importance of the role played by refuge microhabitats in the litter invertebrate recolonisation of burnt sites.

Although our analyses were of insufficient power to detect changes in the relative abundance of microhabitats, they did confirm that most, including fallen logs, survive fire. Fires, particularly the more intense ones, reduced the more common microhabitats but in the process created microhabitats that were typically less common in unburnt sites, and potentially of great importance to rare and relict invertebrate taxa. Both the spring and autumn fires burnt large areas of leaf litter, but also left large pockets of unburnt litter (>10%), often upwind of large logs. Whelan et al. (1980) reported that unburnt patches within a burnt area of jarrah-banksia woodland provided refuges for a greater number of arthropod species and individuals than similar sized unburnt areas. Unburnt litter patches, therefore, may play an important role as refuges both during fire and also in the post-fire litter recovery period. Fallen logs were partly reduced to ashbeds, particularly by the hot autumn fires. Moss swards, a refuge for relict taxa on the dry and infertile jarrah forest floor, occur mostly on these heat sterilised and nutrient rich ashbeds.

Several Australian studies have highlighted the importance of log and moss sward microhabitats as refuges of restricted invertebrate taxa. In south west Australia Main (1987) reported that the relict Midget spiders (Micropholcommatidae) may depend on moss swards on the floor of the jarrah (*E. marginata*) forest for breeding sites. Another relict spider species, the tiny Lungless spider (*Chasmocephalon sp.*), constructs minute orb webs in the ends of fallen logs or burnt-out hollow butt trees in the relict Tingle forest (*E. guilfoylei* and *E. jacksoni*) on the extreme south coast of Western Australia. Taylor (1990) reported that in old logs in a wet sclerophyll forest of southern Tasmania, a suite of invertebrates species may be dependent for their complete life cycle on this restricted log microhabitat. Logs are created when trees and branches fall to the forest floor. Whitford and Williams (1997) found in the jarrah forest of south west Australia that the major cause of tree falls was due to hollowing out of tree butts by fire. The current study showed that the area of the log microhabitat at pre-burnt sites was a very small proportion of the forest floor, while the log ashbeds and moss swards were present in even smaller areas. The dynamic role of spring and intense autumn prescribed fires in both creating logs due to tree falls and the partial destruction of these logs to form ashbeds for moss colonisation is extremely important for the maintenance of microhabitat diversity on the floor of the jarrah forest.

Invertebrates

Seasonal changes in the invertebrate community

Composition of the invertebrate community showed predictable seasonal oscillations, being quite stable over time at the unburnt sites. Similar stability at the ordinal level for surface active arthropods at unburnt sites in dry sclerophyll forest was reported by Neumann and Tolhurst (1991), Collett et al. (1993) and Collett and Neumann (1995). During the 4 year period of this study spring peaks in abundance were dominated by ants and collembolans, with other taxa in the following decreasing rank order: beetles, flies, wasps, spiders, hemipterans, mites and orthopterans, followed by a further 18 uncommon taxa. From early winter to late spring the rapid increase in invertebrates was dominated by decomposers such as collembolans and flies, which had decreased by the onset of late spring. These results agree with those of Hatch (1955), Koch and Majer (1980) and Springett (1976b) who found that the rate of decomposition and the abundance of litter decomposing invertebrates in the northern jarrah forest was higher during winter and spring.

Most taxa had a marked peak in both abundance and average richness in spring. The most speciose taxa at the unburnt sites in spring, in decreasing order, were: ants, wasps, beetles, spiders, flies, hemipterans, mites, collembolans and orthopterans. Spring season peaks are associated with more favourable weather factors, such as moister litter and soil, and higher ambient temperatures. Young, nutrient-rich plant growth is also stimulated by these factors, providing a larger and higher quality food resource for phytophagous invertebrates.

The annual low in abundance and richness found in autumn samples was due largely to a decline in the abundance of ants and collembolans, perhaps explained by a marked reduction in their surface activity. The decline in the surface-activity of ants may be due a reduction in the availability of invertebrate prey and the surface seed bank. While the decline in collembolans was the result of dry litter and soil at this time of year. There were concomitant declines in less numerous taxa. Wasps increased slightly during the autumn period, and became the most speciose group, possible in response to increased abundance of the aestivating hosts of the parasitoid guild. Increased similarity was found between burnt and unburnt sites during autumn, possibly resulting from lower abundances and average richness due to more severe autumn weather conditions. These marked seasonal differences are in agreement with the results of Collett, Neumann and Tolhurst (1993) who found significant changes in the seasonal activity of surface active arthropods in dry sclerophyll forest of west-central Victoria, with abundance being highest in summer and autumn, and lowest in winter.

The strong seasonal effects, and the clear separation of burnt and unburnt sites during spring, highlights the importance of analysing these seasons separately to distinguish fire effects. Average richness in spring was nearly twice that of autumn, and it is reasonable to assume that these additional species may not respond to fire effects in the same manner as the autumn species. The dominance of abundance and sample richness by seasonal effects, suggests that if autumn and spring samples are lumped, this would greatly reduce the sensitivity of BACI analyses to fire effects, especially those apparent in autumn samples. Some taxa responded differently to the conditions of the different seasons; varying responses of the same orders to seasonal effects has the potential to mask any effects of fire. The higher abundances and average richness during spring suggests that analysis of fire effects during this season would provide far more information on the fire responses of a much larger proportion of these litter invertebrate taxa than autumn.

Annual changes in the unburnt invertebrate community

In common with other studies of the impact of fire on litter invertebrate communities, this study illustrates the difficulties of separating the multiple fire responses of the taxa of a complex invertebrate community from the population fluctuations and shifts induced by seasonal or year-to year climatic factors (Friend 1995). Over the 4 year period of this study the unburnt sites had spring peak abundances varying by approximately 30% per year, possibly in response to weather. Over the same 4 year period the spring total sample species richness at these sites remained very stable, with only a 5% change during this period. Many common trends were observed at the majority of sites, regardless of the fire history, and the major causal factor was probably climatic fluctuations. These year-to-year fluctuations are the background against which fire effects should be viewed.

Despite the fluctuations in abundance and richness of each order, detected by the multivariate analyses, there were few changes to the overall structure of the invertebrate community at the long unburnt sites over the four year period of this study. The only taxa to change position in the community structure, based on rankings of abundance, were flies and hemipterans. Flies declined from second most abundant taxon in spring 1992 to seventh in spring 1995. Hemipterans increased from seventh to fifth over the same period. This result concurs with that of Friend and Williams (1996) who found that the abundance changes in Diptera (flies) in mallee-heath of the Stirling Ranges reflected changes following fire, although the largest changes in abundance reflected year-to-year fluctuations. Collett, Neumann and Tolhurst (1993) also reported a decline in Diptera activity, at both unburnt and burnt sites, during the winter following the first of two short rotation prescribed fires in dry sclerophyll eucalypt forest and stated that effects other than fire were the cause.

Species richness, a major component of biodiversity, characterised year-to-year effects at unburnt sites by the magnitude of change in each taxa. Taxa with the greatest richness change, detected by the multivariate analyses, differed for each year of the study. In 1994, at unburnt sites, Apocrita, Araneae, Acarina and Diptera all had relatively large richness increases in either spring or autumn ; in 1995 Thysanoptera and Formicidae had the largest increase and Araneae the largest decrease; and in 1996 Thysanoptera, Blattodea, Orthoptera and Collembola all had large increases. Those taxa useful in distinguishing year-to-year effects on richness were Araneae, Collembola, Thysanoptera, Apocrita, Acarinae, Orthoptera, Blattodea and Formicidae. Only the first three of these were consistently good as indicators, on more than one occasion, but given the vagaries inherent in a short study such as this, it is difficult to conclude that these taxa will always perform consistently. Therefore, to map long-term changes in the species composition of the litter invertebrate community at long unburnt sites it would be necessary to at least monitor the sample richness of the first three of these taxa if not all nine major taxa. The Araneae, Collembola and Thysanoptera contain predatory, decomposer and herbivore guilds which encompasses a broad range of the possible invertebrate responses to year-to-year effects.

Effects of fire

Despite the importance of year-to-year variability in determining changes in the invertebrate community, many taxa responses were clearly linked to fire and could be explained through an understanding of changes in resources, particularly food and habitat, during the two post-fire phases. For example, the higher autumn abundance of the decomposer taxa Isopoda and Pauropoda at the spring burnt sites may have been in response to the greater litter depth and volume remaining after these fires and its possible ameliorating influence on the harsh autumn conditions. Similarly, the high abundance of Formicidae in the first post-fire spring after the high intensity autumn 1993 fire may have been in response to the release of a large quantity of jarrah seed from the scorched crowns. Collembola were also abundant in this situation, possibly due to the post-fire release of litter nutrients and a resultant increase in bacteria and fungal numbers (Warcup 1981). The results found in this study indicate that fungal feeding micro-arthropods such as Collembola had recovered by the first post-fire spring at the autumn burnt sites. By contrast, shortly after the spring 1994 prescribed fires, the abundance of Collembola was markedly reduced, as these fires occurred during the peak activity season of this group. A three month depression in collembola activity following spring fires was also observed by Collett *et al.* (1993) and Campbell and Tanton (1991). Majer (1980) postulated that autumn fires would reduce the numbers of decomposing invertebrates less than spring fires and the results of this study confirmed this effect in the first post-fire spring.

The response by the decomposers, Isopoda and Pauropoda, was the only significant season of burn effect, on the higher taxa, distinguishing the spring and autumn burnt sites. All other fire linked responses detected were common to both burning seasons during the post-fire phases. During the four years post-fire the combine responses of all taxa, measured as total abundance and richness, appeared to be less linked to the immediate impacts of the fires on population sizes and more directly linked to the longer-term recovery of the litter and vegetation resources. This was indicated by the post-fire trends in total abundance and richness which showed small reductions in spring and autumn during the early acute phase, less than a year post-fire, followed by maximum reductions in the early chronic phase, three years post-fire, with reductions becoming less pronounced in the fourth year post-fire. For example, two months after the fires at the spring burnt sites, the late spring-summer active ants and beetles were both more abundant and more diverse than at the unburnt control sites. This increased surface activity may have been due to the simplification of the habitat following combustion of the shrub and litter layer, as well as being the result of the immigration of large numbers of small predatory Acanthocnemid beetles. Whelan *et al.* (1980) also reported a higher abundance and species richness of surface active arthropods at burnt sites several weeks after a wildfire in jarrah-banksia woodland near Perth, south western Australia. By the early chronic phase both beetles and ants had large reductions in abundances, these reductions became less pronounced in the late chronic phase. Similarly, the majority of studies conducted in jarrah forest on the impact of fires on surface- active invertebrates report a recovery to pre-fire numbers of most higher order taxa, however reported recovery periods range from less than three years to more than seven years (Bornemissza 1969, Springett 1976a, Majer 1980, 1984, Abbott 1984, Abbott, Van Heurck and Wong 1984, Abbott and Christensen 1989). Friend (1995) in a review of studies conducted over the last 40 years of fire impacts on surface-active invertebrates in south west and south east temperate Australia concluded that most impacts were only apparent for two to three years after fire.

Richness

Following the fires there was an immediate reduction in richness of Araneae and Apocrita which had large numbers of species in the large sized nomadic predator and pollinator guilds and Acarina with both small sized predators and decomposers. Majer (1984) also reported a short term decline in Araneae following a low intensity autumn fire in the jarrah forest, while Strehlow (1993) reported significant acute impacts following an autumn fire in the semi-arid shrublands of Western Australia's wheatbelt. Similarly, Main and Gaull (1993) found large reductions in the populations of restricted trapdoor spiders following an autumn wildfire on the slopes of the Stirling Ranges.

The large sized herbivores Lepidoptera and Orthoptera , also, had richness reductions during this early phase. All the above reduced taxa had the common attributes of being mostly large sized, nomadic and dependent on larger sized prey or vegetation resources such as live foliage and flowers. These taxa are largely surface-active and may have a more limited availability of refuges during fires, due to their larger size. Their food and habitat resources may take longer to recover, not reaching pre-fire levels until the chronic phase. In contrast, the decomposer, small herbivorous, seed-feeding and scavenging taxa Blattodea, Thysanoptera, Formicidae and Collembola (the last two only in multivariate analyses) had large increases in richness during the acute phase. The decomposer taxa, such as Blattodea and Collembola may have shown a rapid richness increase due to the greater availability and heterogenerity of resources such as soil and litter nutrients and the higher nutrient content of fallen leaves from the scorched tree crowns. The increased richness of the small sized Thysanoptera, which include species from the decomposer and herbivore guilds, may have responded rapidly to the availability of soil and litter nutrients and the small patches of rapidly growing nutrient rich foliage. The seed-feeding Formicidae, also, may have been favoured, in the short-term, by the large quantity of eucalypt seed released from the tree crowns shortly after the fires. Several other studies have reported a short term increase in ant activity following both low intensity and high intensity fires in sclerophyll forests of south east Australia (Neumann 1991, 1992, Collett *et al.* 1993). Majer (1980) also reported that ant species richness was not reduced following a low intensity fire in wandoo woodland in south west Australia.

In the chronic phase, with the near recovery of the litter and vegetation shrub-layer, the Acarina, Orthoptera and Lepidoptera no longer had markedly reduced richnesses. The Araneae and Apocrita, however, still had markedly lower richnesses relative to the unburnt sites. These differing long-term fire responses, again, appear to be linked to the availability of food and habitat resources. The amelioration of the fire impacts on the Acarina, Orthoptera and Lepidoptera may be linked to the availability of small prey, such as collembola in the litter layer, and the increased quantity of nutrient rich foliage, in the case of the Orthoptera and Lepidoptera. The continued richness reduction in the Araneae and Apocrita, during this later phase, may again, reflect a longer recovery of large sized prey or host species (which may only represent a small fraction of the richness of any particular taxa) and also the reduced availability of plant inflorescences. The Blattodea, Thysanoptera and Collembola (this taxon only in multivariate analyses) continued to show favourable responses in richness possibly due to the increased nutrient quality of the litter and vegetation resources or ,perhaps, an ecotonal effect due to the increased heterogenerity of these resources. The Formicidae, during this phase, however, had declined toward the richness at the unburnt sites, possibly due to a short-term decline in seed production and availability at burnt sites. Two additional taxa, the Pauropoda and Dermaptera, had increased to reach richnesses that showed distinct fire responses in this later phase. The Pauropoda are decomposers which may have responded to the increased nutrient availability, while the Dermaptera are saprophagous or predatory species that may have responded to food resource availability and heterogeneity. By the late chronic phase the richnesses of the majority of higher taxa were similar to, or above those of the unburnt sites, which suggested that they were no longer limited by the availability of food or habitat resources.

Abundance

The post-fire changes in litter taxa abundances appeared to largely mirror those of taxa richnesses and again may be linked to changes in food and habitat properties following the fires. During the acute phase a large number of taxa were reduced in abundance, the majority of these were large sized predators, herbivores or pollinators. The reduced taxa were Apocrita, Araneae, Dermaptera, Acarina, Lepidoptera, Orthoptera, Hemiptera and Diptera. Taxa that rapidly responded with increased abundances, during this phase, were Pscoptera, Isopoda, Thysanura, Isoptera, Thysanoptera and Formicidae. The first five of these taxa are largely composed of decomposing species, while the Formicidae are scavengers and seed-feeders. These responses , again, appear to be linked to immediate increases in the availability and quality of their food resources following the fires.

In the chronic phase , the majority of litter taxa no longer showed a distinct reduction in abundance, which suggests food and habitat resources had recovered sufficiently to no longer limit their population sizes or productivity. These taxa were mainly large herbivores or small predators. Taxa that remained reduced in abundance, during this phase, were the Araneae, Dermaptera, Apocrita and Hemiptera. Within these taxa the majority of surface-active litter species may be large sized and predatory, although they do also include saprophagous, parasitoid, pollinator and seed-feeding species. These taxa appear, to still, be limited by the longer recovery time of their food resource or possibly by a slower reproduction capacity or recolonization rate.

In summary, at the higher taxa level, responses to fire appear to be linked to changes in the quality and availability of the food and habitat resources during the post-fire period and not directly to the immediate short-term fire impacts on their population sizes. Decomposer and small herbivore taxa are favoured by resource changes in the acute phase. Large herbivores show immediate declines after the fires, but recover or even increase by the on-set of the chronic phase. Large predators and pollinators, also, respond with immediate declines following the fires and remain at distinctly low numbers in the chronic phase. While, larger sized decomposers, such as Blattodea and Pauropoda, increase in species during the chronic phase. Both the richness and abundance, of the majority of taxa, mirror these fire responses. In addition, at both autumn and spring burnt sites, the majority of higher taxa had similar trophic linked responses to fire. The only season of fire effect, detected, was the higher abundance of decomposing Paropoda and Isopoda at the spring burnt sites in autumn.

Fire Impact on Beetles

Comparison of the beetle trophic structure, of the litter community, at the different post-fire periods suggests that the increased beetle biomass production following the prescribed fires may be translocated up the beetle trophic web in a predictable seral progression from the decomposer guild to the small predatory guild, with a concurrent increase in the herbivore guild by the second post-fire spring, and then to the large predator guild by the fourth post-fire spring. Curculionid morphospecies may be useful indicators of the completion of post-fire recovery in the litter and forest floor invertebrate communities, whereas the predatory tourists Acanthocnemidae were an important indicator of acute fire impacts.

To date few studies in the dry sclerophyll forests of southern Australia have examined the impact of fires on the species of forest floor beetles and none has examined impacts on beetle species biomass. The results of this study have several strong points of agreement with previous studies. A short term (< 2 years) increase in the activity of decomposer/ fungal feeding beetle species and uncommon "minor" beetle families following the first of two spring prescribed fires was reported by Collett and Neumann (1995) in dry sclerophyll forest in south east Australia. In mallee heath in south west Australia, Friend and Williams (1996) reported that predatory Carabid beetles showed a consistent response to fire with a short decline after fire and numbers reaching a maximum in a 40 year old unburnt area. They however attributed the major changes in the Carabid numbers to year-to-year effects.

The impact of fires on beetle morphospecies produced similar responses to those at the order level. In the acute phase the abundance or activity of the small decomposers, such as Hydrophilidae, increased markedly; by the chronic phase the beetle community at burnt sites was greatly simplified with a 50% lower mean sample richness than the unburnt control sites. Although simplified, the composition at the burnt sites was also quite distinct, due to the occurrence of morphospecies apparently restricted to post-fire sites. The beetle morphospecies specific to the post-fire spring burnt sites resulted in these sites having greater total richness, but lower mean sample richness, suggesting a more rapid turnover of morphospecies at these sites. This in turn suggests a seral progression in beetle species composition. Friend and Williams (1996) in contrast indicate that beetle abundance and richness had recovered to unburnt levels within six months of a high intensity wildfire in malle-heath surrounding the Stirling Ranges. Friend (1995) concludes that invertebrates of the drier malle-heaths and woodlands may be more resilient to fires in different seasons than those of the more mesic open forests, such as jarrah forest, due to adaptation to more arid conditions and hence show few season of burn effects.

Fire-induced changes in beetle composition during the chronic phase of this study included an 18-fold increase in beetle biomass at sites burnt in autumn 1993 which may have implications for vertebrates higher up the food web. The presence of beetle morphospecies specific to autumn, spring or long unburnt sites suggests that only a mosaic burning regime could contain and maintain a complete beetle fauna.

Fire response model and bio-indicator groups

We propose the following model of litter invertebrate responses, to single fire events, in the central jarrah forest, based on our findings. Shortly after fire, higher taxa comprised of, large sized predators, pollinators and herbivores, such as Araneae, Apocrita and Orthoptera, had distinct reductions in richness and abundance or activity. In contrast, small decomposers and herbivores such as Pauropoda and Thysanoptera, responded with a distinct increase in richness and abundance, during the acute phase. The small decomposers, also, responded differently to different seasons and/or intensities of burning, with Collembola, initially favoured by a higher intensity autumn fire, while Isopoda and Pauropoda were favoured by the spring fires. By the beginning of the chronic phase, of all burnt sites, large herbivores had recovered or increased, while large sized predators and pollinators remained reduced. By the end of the fourth post-fire year, in the chronic phase, several large sized predator and pollinator taxa remained reduced, while large decomposer and saprophagous taxa had increased in richness and abundance. This chain of responses appears to be strongly linked to post-fire changes in the food and habitat resources.

At the species level, specifically Coleoptera in this study, the responses of trophic guilds mirrored those at the higher taxa level. Coleoptera species responses, also, provided important information on eco-system functions such as biomass production and partitioning; and changes in local species composition during the post-fire period. Coleoptera species had the following responses to fire: immediately following the fire there was a large colonization by a medium sized saprophagous or predatory species, the numbers of this species had returned to pre-fire levels by the end of the acute phase; during the acute phase the small decomposer species markedly increased in abundance and biomass, followed by small predatory species; also, during the acute phase the young leaf herbivore species became more common; lastly, by the beginning of the chronic phase a very large increase in the biomass of large predator species had occurred. These trophic guild responses were, broadly, similar to the responses of the higher taxa.

The eco-system functions, highlighted by the Coleoptera species responses, were the, possibly short-term, increase in productivity that moved up the trophic levels following a fire; and the changed species composition that resulted in a, possible, decline in local species richness, but a increase in regional biodiversity.

Through its detailed examination of the responses of a range of invertebrate taxa to a number of fires, this study is able to shed some light on the use of invertebrate taxa as bio-indicators of fire or other environmental impacts; and for their use in the future testing of the proposed hypotheses, above. No single invertebrate taxon consistently separated year-to-year effects on richness in this study. Rather, we found that a combination of at least the nine most common taxa may be necessary to distinguish and track year-to-year effects, such as climatic change, on richness, over a number of years at unburnt sites. Although, three of these, Araneae, Collembola and Thysanoptera distinguished year-to-year effects, more consistently, in at least two separate years at unburnt sites.

Long term chronic fire impacts at the burnt sites were distinguished from the year-to-year effects by six taxa, while, another three taxa showed responses only during the short term acute phase. The six potential bio-indicator taxa of chronic fire effects were Araneae and Apocrita, with reduced richnesses; and Blattodea, Thysanoptera, Dermaptera and Pauropoda with increased richnesses. The three taxa that had potential as bio-indicators during the acute phase were Orthoptera, Lepidoptera and Acarina, all had reduced richnesses. Five of the these nine taxa that showed a significant fire effect (higher or lower at burnt sites), in the univariate analyses, also, characterised unburnt sites with a increase in richness in the same year. These taxa were Araneae, Apocrita, Acarina, Blattodea and Thysanoptera. This result suggests that favourable year-to-year effects may increase the responsiveness of a taxa to concurrent fire impacts.

The most useful indicator taxa for season of fire effects also varied between years. Orthoptera in 1994 for autumn burnt sites, Coleoptera, Formicidae and Acarina in 1995 for spring and autumn burnt sites, and Collembola in 1996 for autumn burnt sites. Only Isopoda and Pauropoda seemed to offer hope as being consistent indicators across years, but they appeared to be useful in only one analysis and are typically low in abundance.

Friend (1995) concluded in his review that Araneae, Isopoda, Blattodea, Lepidoptera and ,perhaps, Thysanura showed consistent changes in studies of fire impacts in open forest and therefore were potential bio-indicators. The results of this study confirm the bio-indicator potential of Araneae and Blattodea in studying long term fire effects and suggest that Apocrita could also be useful in this regard (see Disney 1986, New 1987). In addition, Coleoptera, Formicidae, Acarina, Collembola, Isopoda and Pauropoda appear to have potential as bio-indicators of fire intensity and/or season of burn effects. These results concur with many of the previous suggestions regarding bio-indicators and highlight several important aspects when detecting fire impacts: first, potential bio-indicator taxa appear to be different for different sampling seasons; second, bio-indicator taxa appear to change from year-to-year; third, taxa that show fire impacts in a particular year also had increased at the control sites, which suggests these taxa may be less limited by annual effects of a particular year and possibly more responsive to fire impacts in the same year. This last aspect, again, suggests that fire is not the major factor determining the composition of the litter invertebrate community during the post-fire period (Friend 1995, Friend and Williams 1996).

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Table 1: Relative percentage change in leaf litter of burnt sites in comparison to unburnt control sites by time since fire. The analysis of variance significant differences are indicated as: *p < 0.05; **p < 0.01.

Litter parameter:	1-4 Years	<1 Year	<2 Years	3-4 Years
% Cover Change:	-21.9358	-32.547	-29.1804	-14.6913
p:	0.07727	0.00200**	0.00571**	0.35800
% Depth Change:	6.4772	-4.953	-7.0166	19.9710
p:	0.53438	0.52490	0.39023	0.16589
% Volume Change:	-22.6570	-32.144	-32.0362	-11.9834
p:	0.20699	0.01819**	0.02287*	0.63226

Table 2:
Mean percentage area of forest floor microhabitats at 14 sites in the Central Jarrah Forest, 2 months before and after low and high intensity autumn and spring prescribed fires. Control, sites 5,6,9,10; Autumn 93, High, sites 13&14; Spring 94, Low, sites 3&4; Spring 94,High, sites 11&12; Autumn 96, Low, sites 1&2; Autumn 96, High, sites 7&8. Total area of each 15m x 15m site is 225 sq. m..
ANOVA level of significance of single degree of freedom contrasts of effects: P<0.05*, <0.01,<0.001***, ns (not significant).**
Magnitude of effects: A>a>B>b.
Direction of effects: "+" is a increase, "-" is a decrease, "0" is no change.

	CONTROL	**AUTUMN 93**		**SPRING 94**				**AUTUMN 96**			
		Fire Intensity:									
		High		**Low**		**High**		**Low**		**High**	
MicroHabitat Type (% area):		**Pre Burn**	**Post Burn**	**Pre Burn**	**Post Burn**	**Pre Burn**	**Post Burn**	**Pre Burn**	**Post Burn**	**Pre Burn**	**Post Bur**
Bare Soil(%):	8.97	----	.17	2.44	2.44	10	10	0	0	1.0	1.0
Unburnt Litter(%):	86.11	----	12.47	96.66	26.97 -B**	84.59	12.5 -a**	94.35	10.03 -A**	93.32	28.1 -b ns
Burnt Litter(%):	0	----	77.27	0	69.70 +B**	0	72.05 +a**	0	83.64 +A**	0	64.9 +b n
Rocks(%):	0	----	.07	0	0	0	0	0	0	0	0
Logs & Branches(%):	4.58	----	8.97	0.54	0.54 0 ns	4.83	4.83 -B ns	3.35	3.06 -a ns	5.11	2.74 -A n
Log Ashbeds(%):	.02	----	.38	0	0 0 ns	0	0 0 ns	1.16	1.76 +a ns	0	2.44 +An
Stumps(%):	.06	----	0	0.28	0.28	.4	.40	.03	.03	.24	0
Stump Holes(%):	0	----	.17	0	0	0	0	.17	.17	.25	.49
Termite Mounds(%):	0	----	0	0	0	0	0	.07	.07	0	0
Moss on Bare Ground(%):	.05	----	0	0	0	.12	.12	0	0	0	0
Moss under Logs(%):	.09	----	.2	0	0	0	0	0	0	0	0
Moss on Ashbeds(%):	.02	----	.17	0	0 0 ns	0	0 0 ns	1.16	1.16 0 ns	0	0 0 ns
Moss on Rocks(%):	0	----	.01	0	0	0	0	0	0	0	0
Moss on Logs(%):	0	----	0	0	0	0	0	.02	.02	.02	.02
Moss at Base of Trunk(%):	.05	----	.07	.04	.04	.04	.03	0.01	0	.04	.09
Moss on Stumps(%):	0	----	0	.03	.03	0	0	0	0	.01	.11
Moss on Termite Mounds(%):	0	----	0	0	0	0	0	.03	.03	0	0
Moss in Stump Holes(%):	0	----	.02	0	0	0	0	0	0	0	0
Total Moss(%):	.21	----	.47	.07	.07 -a ns	0.16	.15 -b ns	1.21	1.21 +Bns	.07	.22 +An

Table 3. The percentage difference in mean abundance per sample of litter invertebrate orders between the unburnt control sites and burnt sites over the 4 year post-fire in the Central Jarrah Forest. Data were analysed using the BACI model of analysis of variance. Significance levels of effects are denoted as: p < 0.1#,p < 0.05*, P < 0.01, p < 0.001***.**

Spring Percentage Abundance of Litter Invertebrates Taxa:				
Taxa:	Post-Fire: 1-4 Years	Early Acute: <1 Year	Acute: <2 Years	Chronic: >2 Years
Araneae:	-25.3	-31.8#	-33.4#	-16.3
		p = 0.084	p = 0.094	
Coleoptera:	-25.5	16.2	-28.0	-22.9
Diptera:	-28.9	-4.7	-7.5	-45.3
Hymenoptera (Apocrita:)	-48.6**	-44.7***	-51.4***	-45.6*
	p = 0.004	p = 0.0008	p = 0.0003	p = 0.039
Ants(Formicidae:)	-1.9	52.4#	24.6	-22.8
		p = 0.072		
Acarina:	-19.0	-26.8	-21.9	-16.1
Collembola:	18.8	-2.8	39.8	0.9
Hemiptera:	-38.8#	-29.7#	-37.9*	-39.7
	p = 0.062	p = 0.057	p = 0.023	
Orthoptera:	-30.9	-46.8#	-15.4	-43.6
		p = 0.060		
Pscoptera	-27.04	-12.5	-24.5#	-29.5
			p = 0.091	
Isopoda	-30.2	5.1#	2.9	-52.7
		p = 0.059		
Thysanura	27.0	37.8*	23.2	31.0
		p = 0.046		
Blattodea	59.8	33.8	28.3	99.0
Isoptera	23.9	52.9#	22.1	25.8
		p = 0.065		
Dermaptera	-29.6#	-2.2	-12.2	-43.6*
	p = 0.057			p = 0.026
Lepidoptera	-23.1	-24.9	-44.1*	5.7
			p = 0.039	
Thysanoptera	80.9#	145.2***	87.2*	74.8
	p = 0.065	p = 0.0008	p = 0.0159	
Total Abundance	-39.5	-7.2	-20.6	-53.9

Autumn Percentage Abundance of Litter Invertebrate Taxa:				
Taxa:	**Post-Fire** Year 1-4	Early Acute <Year 1	Acute <Year 2	Chronic >Year 2
Araneae	-45.7#	-62.8*	-50.7*	-33.9
	p = 0.087	p = 0.016	p = 0.034	
Coleoptera	-39.6	-28.0	-39.4	-40.2
Diptera	-4.2	-38.55#	-13.5	17.3
		p = 0.082		
Hymenoptera (Apocrita)	-42.1	-62.6	-42.5	-41.2
Ants (Formicidae)	47.6	77.7	61.2	23.8
Acarina	117.83	115.83	66.27	273.89
Collembola	0.1	1.6	21.3	-31.9
Hemiptera	-42.7	-64.3#	-52.0	-18.4
		p = 0.069		
Orthoptera	-48.9	-66.6*	-57.0#	-27.5
		p = 0.046	p = 0.066	
Psocoptera	26.4	47.3*	15.4	51.8#
		p = 0.019		p = 0.067
Isopoda	-33.6	28.8	-13.6	-60.8
Thysanura	18.5	36.2	16.6	22.5
Blattodea	6.2	-1.1	-14.1	62.3
Dermaptera	12.9	-23.3	-7.2	67.5
Lepidoptera	10.1	-10.4	-6.7	53.2
Thysanoptera	-8.9	8.6	3.0	-28.7
Pauropoda	25.4	-12.8	-4.6	117.2
Total Abundance	5.4	41.0	27.7	-28.2

Table 4: The impact of spring and autumn prescribed fires on the relative abundance of jarrah forest floor litter invertebrate orders. Data analysed using BACI model of analysis of variance of the relative abundance of spring 94 burnt sites minus the relative abundance of the autumn 93 & 96 burnt sites to determine season of burn effect.

Season of Burn Effects: if effect +ve then spring abundance greater than autumn, if effect -ve then spring abundance less than autumn abundance.

ANOVA level of significance of single degree of freedom contrasts of effects: P<0.10#,<0.05*, <0.01,<0.001***, ns (not significant).**

Taxa:	**Season of Burn Effect: (Spring samples)**	**P**	**Season of Burn Effect: (Autumn samples)**	**P**
Araneae:	+20.5%	0.267 ns	+20.1%	0.359 ns
Coleoptera:	+38.1%	0.218 ns	+58.8%	0.180 ns
Diptera:	+10.2%	0.731 ns	+0.01%	0.980 ns
Hymenoptera: (wasps)	-5.7%	0.638 ns	+33.8%	0.336 ns
Hymenoptera: (ants)	+23.2%	0.222 ns	-23.9%	0.362 ns
Acarina:	+32.7%	0.122 ns	+0.02%	0.962 ns
Collembola:	-17.4%	0.629 ns	+0.01%	0.972 ns
Hemiptera:	-5.3%	0.733 ns	+27.2%	0.407 ns
Orthoptera:	-36.3%	0.175 ns	+17.1%	0.587 ns
Pscoptera:	-0.8%	0.951 ns	+5.4%	0.552 ns
Isopoda:	+35.4%	0.091 # ns	+51.1%	0.025 *
Thysanura:	+2.8%	0.828 ns	+7.9%	0.609 ns
Blattodea:	+6.2%	0.815 ns	-11.1%	0.680 ns
Isoptera:	+22.9%	0.234 ns	-	-
Dermaptera:	+14.4%	0.141 ns	+7.7%	0.665 ns
Lepidoptera:	+22.8%	0.271 ns	+8.6%	0.676 ns
Thysanoptera:	-15.5%	0.405 ns	+17.6%	0.246 ns
Pauropoda:	-	-	+56.0%	0.0184 *
Total Abundance:	+37.8%	0.294 ns	+28.5%	0.0686 #

Table 5:The percentage difference in morphospecies richness per sample of litter invertebrate taxa between unburnt sites and burnt sites over the 4 year post-fire period in the Central Jarrah Forest.Data was analysed using the BACI model of analysis of variance for spring or autumn seasons. Significance levels of effects are denoted as: $p < 0.1$#,$p < 0.05$*, $P < 0.01$**, $p < 0.001$***.

RICHNESS-SPRING Samples:				
	Percentage Difference from Controls:			
Taxa:	Post-Fire 1-4 years:	Early Acute <1 years:	Acute <2 years:	Chronic >2 years:
Araneae:	-62.9*	-56.8*	-60.9*	-64.8#
	*0.048	*0.013	*0.015	#0.082
Coleoptera:	-31.1	0.96	22.4	-38.9
Diptera:	-15.9	-7.0	-10.7	-20.7
Hymenoptera (Apocrita):	-55.7*	-49.4**	-56.5**	-54.8#
	*0.019	**0.005	**0.004	#0.057
Ants (Formicidae):	-9.4	24.1	6.5	-22.9
Acarina:	-50.2	-43.3#	-47.5#	-52.8
		#0.061	#0.066	
Collembola:	4.107	6.598	1.284	7.008
Hemiptera:	-11.0	3.1	-5.8	-15.8
Orthoptera:	11.0	7.3	22.5	0.6
Pscoptera:	-22.9	-9.9	-20.7	-25.0
Isopoda:	-24.3	28.4	1.9	-43.8
Thysanura:	-9.9	19.5	1.4	-20.0
Blattodea:	95.0#	57.0#	59.2#	138.9#
	#0.067	#0.059	#0.087	#0.065
Isoptera:	-26.5	-1.0	-19.8	-32.8
Dermaptera:	-37.9	-9.6	-22.8	-50.0
Lepidoptera:	-41.6	-34.4	-50.7#	-30.8
			#0.086	
Thysanoptera:	138.7*	138.3**	122.3*	156.3#
	*0.042	**0.005	*0.019	#0.078
Total Richness:	-26.4	-9.5	-21.4	-31.2

Table 5: continued.

RICHNESS-AUTUMN SAMPLES:				
	Percentage Difference from Controls:			
Taxa:	Post-Fire 1-4 years:	Early Acute <1 years:	Acute <2 years:	Chronic >2 years:
Araneae:	-21.6	-55.2	-36.4	19.3
		*0.047		
Coleoptera:	2.7	-11.3	-12.0	40.2
Diptera:	-0.3	-25.2	1.2	-3.4
Hymenoptera: (Apocrita)	-14.8	-40.5	-21.4	-0.1
Hymenoptera: (Formicidae)	18.5	25.7	18.2	19.1
Acarina:	72.1	45.8	50.5	125.1
Collembola:	11.1	5.9	8.1	17.2
Hemiptera:	4.9	-31.5	-6.8	33.0
Orthoptera:	-33.1	-56.7	-44.3	-3.4
		**0.010	*0.030	
Pscoptera:	26.6	32.2	12.5	60.4
Isopoda:	-4.3	21.0	3.1	-17.7
Thysanura:	21.4	28.8	16.3	32.2
Blattodea:	-13.8	10.6	-11.4	-18.6
Dermaptera:	43.7	-18.2	7.4	157.3
	#0.098			**0.017
Lepidoptera:	11.3	-6.1	0.1	37.6
Thysanoptera:	-11.1543	8.4511	-2.5611	-26.134
Pauropoda:	42.5	2.7	14.9	119.0
				*0.057
Total Richness:	6.0	-9.8	-1.8	23.8
	0.66464	0.42911	0.86794	0.34485

Table 6: The invertebrate taxa trapped from November 1992 to November 1996 at autumn 1993 burnt sites, spring 1994 burnt and unburnt control sites before and after the spring and autumn prescribed fires. (X = trapped at least once in specified period).

Invertebrate Taxon:	*Trophic & Size Guilds	Post-Autumn 1993 Burnt Sites	Pre-Spring 1994 Burn Period		Post-Spring 1994 Burn Period	
			Spring 1994 Burnt Sites	Unburnt Control Sites	Spring 1994 Burnt Sites	Unburnt Control Sites
Araneae: (spiders) 1:	Small-large predators	X	X	...X	...X	X
Coleoptera: (beetles) 2:	Varied guilds	...X	...X	...X	...X	...X
Diptera: (flies) 3:	Varied guilds	...X	...X	...X	...X	...X
Apocrita: (Wasps) 4:	Parasitoids Predators Pollinators	...X	...X	...X	...X	...X
Formicidae: (ants) 5:	Medium Omnivores sap & seed	X	X	X	X	X
Acarina: (mites) 6:	Small Predators Decomposers	X	X	X	X	X
Collembola: (springtails) 7:	Small Decomposers	X	X	X	X	X
Hemiptera: (bugs) 8:	Medium Sapfeeders Predators	X	X	X	X	X
Orthoptera: (crickets & grasshoppers) 9:	Large Decomposers Herbivores Predators	X	X	X	X	X
Pscoptera: (booklice) 10:	Small Decomposers	X	X	X	X	X
Scorpionida: (scorpions) 11:	Large Predators	X	X	X	X	X
Isopoda: (woodlice) 12:	Medium Decomposers	X	X	X	X	X
Chilopoda: (centipedes) 13	Large Predators	X	X	X	X	X
Thysanura: (silverfish) 14:	Medium Decomposers	X	X	X	X	X
Blattodea: (cockroaches) 15:	Large Omnivores	X	X	X	X	X
Mantodea: (mantids) 16:	Large Predators	X	X		X	X
Isoptera: (termites) 17:	Medium Decomposers	X	X	X	X	X

Table 6: (continued from previous page):

Dermaptera: (earwigs) 18:	Medium Predators	X	X	X	X	X
Lepidoptera: (caterpillars) 19:	Medium - Large Herbivores	X	X	X	X	X
Thysanoptera: (thrips) 20:	Small Herbivores Predators	X	X	X	X	X
Pseudoscorpionida (pseudoscorpions) 21:	Small Predators	X	X	X	X	X
Opilionida: (harvestmen) 22:	Medium Predators	X	X	X	X	
Diplura: (diplurans) 23:	Small Herbivores Predators	X	X	X	X	X
Pauropoda: (pauropods) 24:	Small Decomposers	X	X	X	X	X
Gastropoda: (snails) 25:	Small Omnivores	X	X	X		X
Symphyla: (symphlans) 26:	Small Decomposers Predators		X			
Oligochaeta: (earthworms) 27:	Medium - Large Decomposers	X	X	X		
Tricladida: (flatworms) 28:	Medium Predators	...X	X			
Neuroptera: (Lacewings) 29:	Large Predators	X		X		
Hoplonemertea: (nematodes) 30:	Small Predators					
Embioptera: (web-spinners) 31:	Medium Herbivores	X			X	
Mecoptera: (scorpionflies) 32:	Medium Predators	X				
Diplopoda: (millipedes) 33:	Medium - Large Decomposers	X				
Total Taxa:		31	28	26	25	24

* Trophic guilds adapted from Harvey and Yen (1989).

Table 7: Seasonal sample richness of litter invertebrate morphospecies captured at the control and pre-fire spring 94 prescribed fire sites from May 93 to November 95.

Season:	SPRING:		SUMMER		AUTUMN		WINTER
Number of samples:	32		16		48		80
All morphospecies per sample (Mean only)							
Taxon:							
Araneae (Spiders)	9.06		6.31		6.97		6.36
Coleoptera (Beetles)	11.03		5.5		6.1		8.62
Diptera (Flies)	9.03		2.43		5.87		6.75
Hymenoptera (Wasps)	12.49		7.68		9.31		6.56
Formicidae (Ants)	15.27		14.00		7.68		6.97
Acarina (Mites)	6.99		5.00		3.77		4.80
Collembola (Spring-Tails)	6.34		3.31		4.31		6.07
Hemiptera (Bugs)	8.06		4.18		4.52		2.93
Orthoptera (Crickets & Grasshoppers	1.84		1.31		1.67		1.54
All Minor Taxa	9.69		4.33		5.46		4.08
Total Richness	89.81		54.05		54.99		55.13

Table 8: The morphospecies richness and trophic guilds of beetle families at unburnt control sites and sites burnt in autumn 1993 and spring 1994 trapped in November 1994 and November 1996.

Taxa & Family:	**Sample Rich.** **Nov.94 Autumn 93**	**Sample Rich.** **Nov.96 Autumn 93**	**Sample Rich.** **Nov.94 Control**	**Sample Rich.** **Nov.94 Spring 94**	**Sample Rich.** **Nov.96 Control:**	**Sample Rich.** **Nov.96 Spring 94**	**Total Rich.**
Decomposer Taxa: a							
Mycteridae	1	0	2	4	1		5
Hydrophilidae	3	1	2	2	1	2	3
Silvanidae			1				1
Mordellidae			1	1	1		1
Nitidulidae	2		1	3			4
Tenebrionidae	1		2	1	1	1	3
Pythidae	1						1
Decomposers Totals:	**8**	**1**	**9**	**11**	**4**	**3**	**18**
Saprophagus Taxa:							
Anthicidae	1	1		1			2
Dermestidae	1	1	2	2	1		4
Saprophages Totals:	**2**	**2**	**2**	**3**	**1**	**0**	**6**
Fungivore Taxa:							
Ptiliidae		1	2	2	3		4
Lathridiidae	1		1	1			1
Languriidae	1	1					1
Corylophidae					1		1
Colydiidae				1			1
Salpingidae	1	2	1	2	1	1	4
Fungivores Totals:	**3**	**4**	**4**	**6**	**5**	**1**	**12**
Herbivore Taxa:							
Byrrhidae					1		1
Chrysomelidae	4	1	2	9	2	2	14
Curculionidae	5	3	6	7	5	3	18
Gonipterinae					1		1
Amycterinae			1	1			2
Scarabaeidae			2	2	2	1	4
Herbivores Totals:	**9**	**4**	**11**	**19**	**11**	**6**	**40**
Woodborers Taxa:							
Bostrichidae						1	1
Anobiidae	1	1	2	3	1	1	4
Woodborers Totals:	**1**	**1**	**2**	**3**	**1**	**2**	**5**
Omnivore Taxa:							
Cantharidae		1	2				2
Elateridae	2			1	1		4
Omnivores Totals:	**2**	**1**	**2**	**1**	**1**	**0**	**6**

Table 8 (continued from previous page.)

Taxa & Family:	**Sample Richness** **Nov.94 Autumn 93**	**Sample Richness** **Nov.96 Autumn 93**	**Sample Richness** **Nov.94 Control**	**Sample Richness** **Nov.94 Spring94**	**Sample Richness** **Nov.96 Control:**	**Sample Richness** **Nov.96 Spring 94**	**Total Richness**
Small Predator Taxa:							
Pselaphidae	6		8	11	5	3	15
Staphylinidae	5	3	9	10	6	7	18
Scydmaenidae	2		4	3		1	6
Cleridae	1						3
Small Predators Totals:	**14**	**3**	**21**	**24**	**11**	**11**	**42**
Large Predator Taxa:							
Carabidae		2	3	6			11
Large Predators Totals:	**0**	**2**	**3**	**6**	**0**	**0**	**11**
Parasitoid Taxa:							
Rhipiphoridae			1	3	1		3
Parasitoids Totals:	**0**	**0**	**1**	**3**	**1**	**0**	**3**
Aquatic Predator Taxa:							
Dytiscidae					1		1
Aquatic Predators Totals:	**0**	**0**	**0**	**0**	**1**	**0**	**1**
Unknown Trophic Taxa:							
Coleoptera						1	4
Acanthocnemidae	1	1	1	1	1	1	1
Unknown Trophic Level Totals:	**1**	**1**	**1**	**1**	**1**	**2**	**5**
Total Families:	**19**	**13**	**22**	**23**	**20**	**13**	**33**
Richness for Treatment Sites:	**40**	**19**	**56**	**77**	**37**	**25**	**149**

a) Adapted from Collet and Newmann(1995) , Lawrence and Britton (1991).

Table 9: The mean abundance per sample and trophic guilds of beetle families at unburnt control sites and sites burnt in autumn 1993 and spring 1994 trapped in November 1994 and November 1996.

Taxa & Family:	Mean Abund. Nov.94 Autumn 93	Mean Abund. Nov.96 Autumn 93	Mean Abund. Nov.94 Control	Mean Abund. Nov.94 Spring 94	Mean Abund. Nov.96 Control:	Mean Abund. Nov.96 Spring 94	Total Abundance.
Decomposer Taxa:							
Mycteridae	0.5	0	0.25	0.56	0.5	0	19
Hydrophilidae	5.75	4	19.81	67.62	1.75	0.5	1462
Silvanidae	0	0	0.06	0	0	0	1
Mordellidae	0	0	0.06	0.06	0.5	0	4
Nitidulidae	0.38	0	0.19	0.5	0	0	14
Tenebrionidae	0.13	0	0.31	0.19	0.25	0.75	13
Pythidae	0.13	0	0	0	0	0	1
Decomposers Totals:	**6.89**	**4**	**20.68**	**68.93**	**3**	**1.25**	**1514**
Saprophagus Taxa:							
Anthicidae	0.38	2	0	0.06	0	0	8
Dermestidae	1	0.5	0.5	0.75	0.5	0	31
Saprophages Totals:	**1.38**	**2.5**	**0.5**	**0.81**	**0.5**	**0**	**39**
Fungivore Taxa:							
Ptiliidae	0	0.5	0.19	0.37	1.25	0	15
Lathridiidae	0.25	0	0.13	0.06	0	0	5
Languriidae	0.13	0.5	0	0	0	0	2
Corylophidae	0	0	0	0	0.5	0	2
Colydiidae	0	0	0	0.19	0	0	3
Salpingidae	0.13	1	0.31	2.5	1.25	0.25	54
Fungivores Totals:	**0.51**	**2**	**0.63**	**3.12**	**3**	**0.25**	**81**
Herbivore Taxa:							
Byrrhidae	0	0	0	0	0.25	0	1
Chrysomelidae	0.5	0.5	0.37	1.12	0.5	0.5	33
Curculionidae	1	2.5	0.94	1	2.5	1.5	60
Gonipterinae	0	0	0	0	0.25	0	1
Amycterinae	0	0	0.06	0.06	0	0	2
Scarabaeidae	0	0	0.5	0.18	0.75	0.25	15
Herbivores Totals:	**1.5**	**3**	**1.87**	**2.36**	**4.25**	**2.25**	**112**
Woodborers Taxa:							
Bostrichidae	0	0	0	0	0	0.25	1
Anobiidae	0.13	1	0.69	0.19	0.25	0.25	19
Woodborers Totals:	**0.13**	**1**	**0.69**	**0.19**	**0.25**	**0.5**	**20**
Omnivore Taxa:							
Cantharidae	0	0.5	0.25	0	0	0	5
Elateridae	0.25	0	0	0.19	0.5	0	7
Omnivores Totals:	**0.25**	**0.5**	**0.25**	**0.19**	**0.5**	**0**	**12**

Taxa & Family:	**Mean Abund.**	**Mean Abund.**	**Mean Abund.**	**Mean Abund.**	**Mean Abund.**	**Mean Abund.**	
	Nov.94 Autumn 93	**Nov.96 Autumn 93**	**Nov.94 Control**	**Nov.94 Spring 94**	**Nov.96 Control:**	**Nov.96 Spring 94**	**Total Abundance.**
Small Predator Taxa:							
Pselaphidae	1	0	8.6	9.62	2	1.25	313
Staphylinidae	1.62	10	5.12	1.87	4.25	4.25	179
Scydmaenidae	0.38	0	1.12	2	0	0.25	54
Cleridae	0.13	0	0	0	0	0	1
Small Predators Totals:	**3.13**	**10**	**14.84**	**13.49**	**6.25**	**5.75**	**547**
Large Predator Taxa:							
Carabidae	0	1	0.19	0.82	0	0	18
Large Predators Totals:	**0**	**1**	**0.19**	**0.82**	**0**	**0**	**18**
Parasitoid Taxa:							
Rhipiphoridae	0	0	0.06	0.37	0.25	0	8
Parasitoids Totals:	**0**	**0**	**0.06**	**0.37**	**0.25**	**0**	**8**
Aquatic Predator Taxa:							
Dytiscidae	0	0	0	0	0.25	0	1
Aquatic Predators Totals:	**0**	**0**	**0**	**0**	**0.25**	**0**	**1**
Unknown Trophic Taxa:							
Coleoptera	0	0	0	0	0	0.25	1
Acanthocnemidae	18.87	0.5	1.25	64.37	0.25	0.25	1204
Unknown Trophic Level Totals:	**18.87**	**0.5**	**1.25**	**64.37**	**0.25**	**0.5**	**1205**
Mean Total Beetles per Sample:	**34.55**	**29**	**42.09**	**158.58**	**22**	**10.75**	**3557**
Total Families:	**19**	**13**	**22**	**23**	**20**	**13**	**33**

Table 10: The biomass (mean volume per sample, cu.mm.) and trophic guilds of beetle families at unburnt control sites and sites burnt in autumn 1993 and spring 1994 trapped in November 1994 and November 1996.

Taxa & Family:	Mean Volume Nov.94 Autumn 93	Mean Volume Nov.96 Autumn 93	Mean Volume Nov.94 Control	Mean Volume Nov.94 Spring94	Mean Volume Nov.96 Control:	Mean Volume Nov.96 Spring 94	Total Volume (cu. mm)	Estimated Biomass /sq. metre/day (cu.mm.)
Decomposer Taxa:								
Mycteridae	0.1	0	0.11	0.13	0.104	0	5.056	6.3
Hydrophilidae	2.9	1.79	8.94	30.63	0.78	0.29	664.18	830.2
Silvanidae	0	0	0.11	0		0	1.76	2.2
Mordellidae	0	0	0.039	0.29	1.15	0	9.864	12.3
Nitidulidae	0.84	0	1.2	2.63		0	68	85
Tenebrionidae	0.31	0	3.91	1.94	3.28	9.8	148.4	185.5
Pythidae	2.92	0		0		0	23.36	29.2
Decomposers Totals:	**7.07**	**1.79**	**14.309**	**35.62**	**5.314**	**10.09**	**920.62**	**1150.8**
Saprophagus Taxa:								
Anthicidae	3.64	19.44		0.08		0	69.28	86.6
Dermestidae	0.07	0.13	0.26	0.67	0.294	0	16.876	21.1
Saprophages Totals:	**3.71**	**19.57**	**0.26**	**0.75**	**0.294**	**0**	**86.156**	**107.7**
Fungivore Taxa:								
Ptiliidae	0	0.26	0.07	0.14	0.7	0	6.68	8.4
Lathridiidae	0.08	0	0.039	0.01		0	1.424	1.8
Languriidae	0.07	0.29		0		0	1.14	1.4
Corylophidae	0	0		0	0.396	0	1.584	1.9
Colydiidae	0	0		0.44		0	7.04	8.8
Salpingidae	0.44	0.38	0.24	1.84	0.94	0.19	42.08	52.6
Fungivores Totals:	**0.59**	**0.93**	**0.349**	**2.43**	**2.036**	**0.19**	**59.948**	**74.9**
Herbivore Taxa:								
Byrrhidae	0	0		0	0.012	0	0.048	0.06
Chrysomelidae	18.96	0.05	1.1	19.98	0.59	8.49	525.38	656.7
Curculionidae	2.49	7.51	6.94	9.54	4.54	5.72	339.66	424.6
Gonipterinae	0	0		0	4.06	0	16.24	20.3
Amycterinae	0	0	9.41	3.75		0	210.56	263.2
Scarabaeidae	0	0	229.43	4.96	19.83	31.02	3953.64	4942.0
Herbivores Totals:	**21.45**	**7.56**	**246.88**	**38.23**	**29.032**	**45.23**	**5045.528**	**6306.9**
Woodborers Taxa:								
Bostrichidae	0	0		0		0.15	0.6	0.8
Anobiidae	0.08	0.68	0.503	0.36	0.34	0.31	18.408	23.0
Woodborers Totals:	**0.08**	**0.68**	**0.503**	**0.36**	**0.34**	**0.46**	**19.008**	**23.8**

Table 10: (continued from previous page.)

Taxa & Family:	**Mean Volume**	**Mean Volume**	**Mean Volume**	**Mean Volume**	**Mean Volume**	**Mean Volume**		**Estimated Biomass**
	Nov.94 Autumn 93	**Nov.96 Autumn 93**	**Nov.94 Control**	**Nov.94 Spring94**	**Nov.96 Control:**	**Nov.96 Spring 94**	**Total Volume (cu. mm)**	**/sq. metre/day (cu.mm.)**
Omnivore Taxa:								
Cantharidae	0	9.99	3.74	0		0	79.82	99.8
Elateridae	4.04	0		5.51	0.7	0	123.28	154.1
Omnivores Totals:	**4.04**	**9.99**	**3.74**	**5.51**	**0.7**	**0**	**203.1**	**253.8**
Small Predator Taxa:								
Pselaphidae	0.59	0.18	11.34	4.54	2.74	1.37	275.6	344.5
Staphylinidae	1.52	43.88	17.99	5.15	15.95	17.54	604.12	755.2
Scydmaenidae	0.34	0	1.09	2.77		0.02	64.56	80.7
Cleridae	0.54	0		0		0	4.32	5.4
Small Predators Totals:	**2.99**	**44.06**	**30.42**	**12.46**	**18.69**	**18.93**	**948.6**	**1185.8**
Large Predator Taxa:								
Carabidae	0	1401.66	1.83	33.06		0	3361.56	4201.9
Large Predators Totals:		**1401.66**	**1.83**	**33.06**	**0**	**0**	**3361.56**	**4201.9**
Parasitoid Taxa:								
Rhipiphoridae	0	0	0.049	0.31	0.19	0	6.504	8.1
Parasitoids Totals:	**0**	**0**	**0.049**	**0.31**	**0.19**	**0**	**6.504**	**8.1**
Aquatic Predator Taxa:								
Dytiscidae	0	0		0	24.65	0	98.6	123.2
Aquatic Predators Totals:	**0**	**0**	**0**	**0**	**24.65**	**0**	**98.6**	**123.2**
Unknown Trophic Taxa:								
Coleoptera	0	0		0		0.01	0.04	0.05
Acanthocnemidae	35.33	0.93	2.34	120.51	0.47	0.47	2253.86	2817.3
Unknown Totals:	**35.33**	**0.93**	**2.34**	**120.51**	**0.47**	**0.48**	**2253.9**	**2817.4**
Mean Volume : (per sample)	**75.26**	**1487.17**	**300.68**	**249.24**	**81.716**	**115.83**		
Total Volume of Beetles (cu. mm) :							**13003**	
Estimated Biomass: /sq.m./day (cu.mm):	**94.1**	**1858.9**	**375.8**	**311.6**	**102.1**	**144.8**		**16253.8**

Table 11: Beetle morphospecies of unburnt control sites and sites prescribed burnt in autumn 1993 and spring 1994. Beetle morphospecies were determined for samples trapped in November 1994 and November 1996.

Taxa & Families:	Morpho Species	Richness	Autumn 93	Autumn 93	Controls	Controls	Spring 94	Spring 94
			Nov.94	Nov.96	Nov.94	Nov.96	Nov.94	Nov.96
Acanthocnemidae	366		X		X	X	X	X
Acanthocnemidae Total		1						
Amycterinae	468				X			
Amycterinae	470						X	
Amycterinae Total		2						
Anobiidae	248		X	X	X	X	X	
Anobiidae	431						X	
Anobiidae	446				X			X
Anobiidae	474						X	
Anobiidae Total		4						
Anthicidae	29		X	X	X			
Anthicidae	438						X	
Anthicidae Total		2						
Bostrichidae	510							X
Bostrichidae Total		1						
Byrrhidae	506					X		
Byrrhidae Total								
Cantharidae	445			X	X			
Cantharidae	450				X			
Cantharidae Total		2						
Carabidae	266				X			
Carabidae	271				X			
Carabidae	295			X				
Carabidae	364						X	
Carabidae	396						X	
Carabidae	419						X	
Carabidae	420						X	
Carabidae	432						X	
Carabidae	469				X			
Carabidae	471						X	
Carabidae	492			X				
Carabidae Total		11						

Taxa & Families:	**Morpho Species**	**Richness**	**Autumn 93**	**Autumn 93**	**Controls**	**Controls**	**Spring 94**	**Spring 94**
			Nov.94	**Nov.96**	**Nov.94**	**Nov.96**	**Nov.94**	**Nov.96**
Chrysomelidae	56		X					
Chrysomelidae	215						X	
Chrysomelidae	254			X				
Chrysomelidae	257				X			
Chrysomelidae	267							X
Chrysomelidae	273					X		
Chrysomelidae	376						X	
Chrysomelidae	389		X		X		X	
Chrysomelidae	412		X					
Chrysomelidae	423						X	
Chrysomelidae	425						X	
Chrysomelidae	426						X	
Chrysomelidae	430						X	
Chrysomelidae	509						X	
Chrysomelidae Total		14						
Cleridae	410		X					
Cleridae	441				X			
Cleridae	444				X			
Cleridae Total		3						
Coleoptera	261							X
Coleoptera	415				X			
Coleoptera	463				X			
Coleoptera	464				X			
Coleoptera Total		4						
Colydiidae	439						X	
Colydiidae Total		1						
Corylophidae	281					X		
Corylophidae Total		1						

Taxa & Families:	Morpho Species	Richness	Autumn 93	Autumn 93	Controls	Controls	Spring 94	Spring 94
			Nov.94	Nov.96	Nov.94	Nov.96	Nov.94	Nov.96
Curculionidae	245		X		X			
Curculionidae	259					X		
Curculionidae	260			X				
Curculionidae	261				X			
Curculionidae	274		X					
Curculionidae	276					X		
Curculionidae	297			X				
Curculionidae	297				X			
Curculionidae	399		X	X	X	X	X	X
Curculionidae	407		X				X	
Curculionidae	413		X				X	
Curculionidae	418						X	
Curculionidae	421						X	
Curculionidae	443				X			
Curculionidae	448				X		X	
Curculionidae	501							X
Curculionidae	502							X
Curculionidae Total		17						
Dermestidae	255						X	
Dermestidae	293		X		X	X	X	
Dermestidae	373			X				
Dermestidae	391				X			
Dermestidae Total		4						
Dytiscidae	505				X			
Dytiscidae Total		1						
Elateridae	286		X		X	X		
Elateridae	436						X	
Elateridae	462				X			
Elateridae Total		3						
Gonipterinae	507					X		
Gonipterinae Total		1						
Hydrophilidae	30		X	X	X	X	X	X
Hydrophilidae	252		X		X		X	X
Hydrophilidae	408							
Hydrophilidae Total		3						
Languriidae	411		X	X				
Languriidae Total		1						

Taxa & Families:	Morpho Species	Richness	Autumn 93	Autumn 93	Controls	Controls	Spring 94	Spring 94
			Nov.94	Nov.96	Nov.94	Nov.96	Nov.94	Nov.96
Lathridiidae	275							X
Lathridiidae	414		X		X			
Lathridiidae Total		2						
Mordellidae	262				X	X	X	
Mordellidae Total		1						
Mycteridae	246		X		X	X	X	
Mycteridae	264						X	
Mycteridae	435						X	
Mycteridae	447				X			
Mycteridae	473						X	
Mycteridae Total		5						
Nitidulidae	402		X		X		X	
Nitidulidae	405		X					
Nitidulidae	417						X	
Nitidulidae	429						X	
Nitidulidae Total		4						
Pselaphidae	195					X	X	
Pselaphidae	234		X					
Pselaphidae	244				X	X	X	X
Pselaphidae	249				X		X	
Pselaphidae	250		X		X		X	
Pselaphidae	285			X	X		X	
Pselaphidae	287		X		X	X	X	
Pselaphidae	371				X		X	X
Pselaphidae	372		X		X		X	
Pselaphidae	387						X	
Pselaphidae	388					X		
Pselaphidae	406		X					
Pselaphidae	416						X	
Pselaphidae	427				X		X	
Pselaphidae	442				X			
Pselaphidae Total		15						
Ptiliidae	143			X		X	X	
Ptiliidae	394				X		X	
Ptiliidae	467					X		
Ptiliidae	503					X		
Ptiliidae Total		4						
Pythidae	404		X					
Pythidae Total		1						

Taxa & Families:	Morpho Species	Richness	Autumn 93 Nov.94	Autumn 93 Nov.96	Controls Nov.94	Controls Nov.96	Spring 94 Nov.94	Spring 94 Nov.96
Rhipiphoridae	263					X	X	
Rhipiphoridae	273						X	
Rhipiphoridae	434						X	
Rhipiphoridae Total		3						
Salpingidae	288			X				
Salpingidae	367		X					
Salpingidae	393			X	X	X	X	X
Salpingidae	424						X	
Salpingidae Total		4						
Scarabaeidae	256				X	X	X	
Scarabaeidae	375					X	X	
Scarabaeidae	466					X		
Scarabaeidae	508							X
Scarabaeidae Total		4						
Scydmaenidae	140				X		X	
Scydmaenidae	253							X
Scydmaenidae	258		X		X		X	
Scydmaenidae	401		X		X			
Scydmaenidae	433						X	
Scydmaenidae	449				X			
Scydmaenidae Total		6						
Silvanidae	465				X			
Silvanidae Total		1						
Staphylinidae	31					X	X	
Staphylinidae	32		X		X	X	X	
Staphylinidae	33						X	
Staphylinidae	36			X		X		
Staphylinidae	141					X		X
Staphylinidae	251		X	X	X	X	X	X
Staphylinidae	301				X		X	
Staphylinidae	303			X				X
Staphylinidae	377		X		X		X	X
Staphylinidae	379		X					X
Staphylinidae	400						X	
Staphylinidae	409		X					
Staphylinidae	422				X	X	X	
Staphylinidae	428						X	
Staphylinidae	460				X			
Staphylinidae	461				X			X
Staphylinidae	488							X
Staphylinidae Total		17						

Taxa & Families:	**Morpho Species**	**Richness**	**Autumn 93 Nov.94**	**Autumn 93 Nov.96**	**Controls Nov.94**	**Controls Nov.96**	**Spring 94 Nov.94**	**Spring 94 Nov.96**
Tenebrionidae	386				X	X		X
Tenebrionidae :		1						
Morphospecies: Total:		**149**						
Families Total:		**33**						

Morphospecies Only at:	**Autumn 93 Burnt:**	**Controls:**	**Spring 94 Burnt:**
	18	29	39
	Burnt:		**Unburnt:**
	60		29

Families Only at:	**Autumn 93 Burnt:**	**Controls:**	**Spring 94 Burnt:**
	2	5	6
	Burnt:		**Unburnt:**
	11		5

Fig.12. Principal Components Biplots (PCA) comparing relative abundance in spring of unburnt sites with burnt sites by time since fire. Open squares = unburnt sites; filled stars = spring 1994 burnt sites; filled diamonds = autumn 1993 & 96 burnt sites. Numeric labels indicate years since fire.

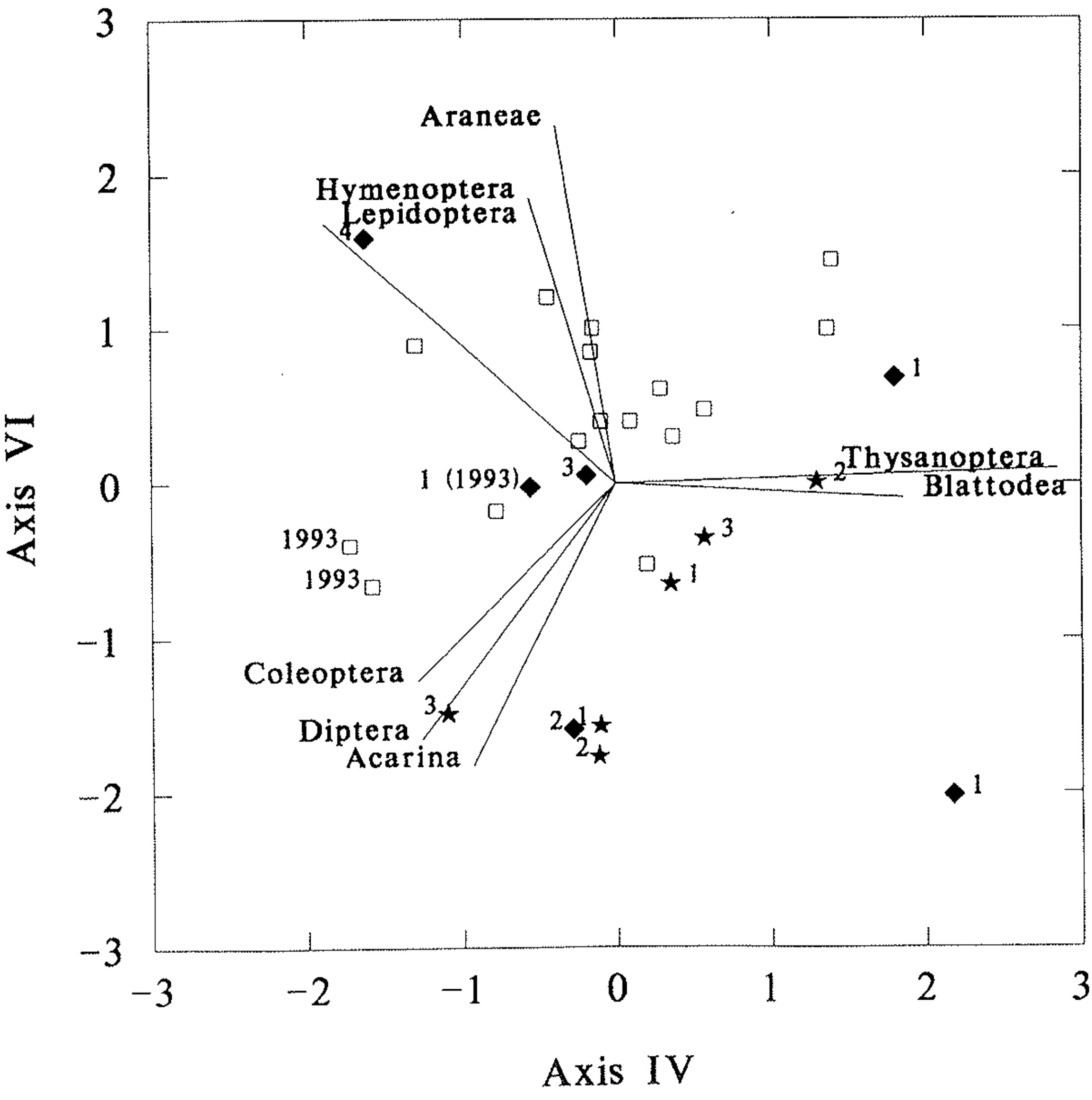


Fig.13. Principal Components Biplots comparing relative abundance in autumn of unburnt sites with burnt sites by year of sample. Open circles = unburnt sites; Filled circles = autumn 1993 & spring 1994 burnt sites. Numeric labels indicate year of sample.

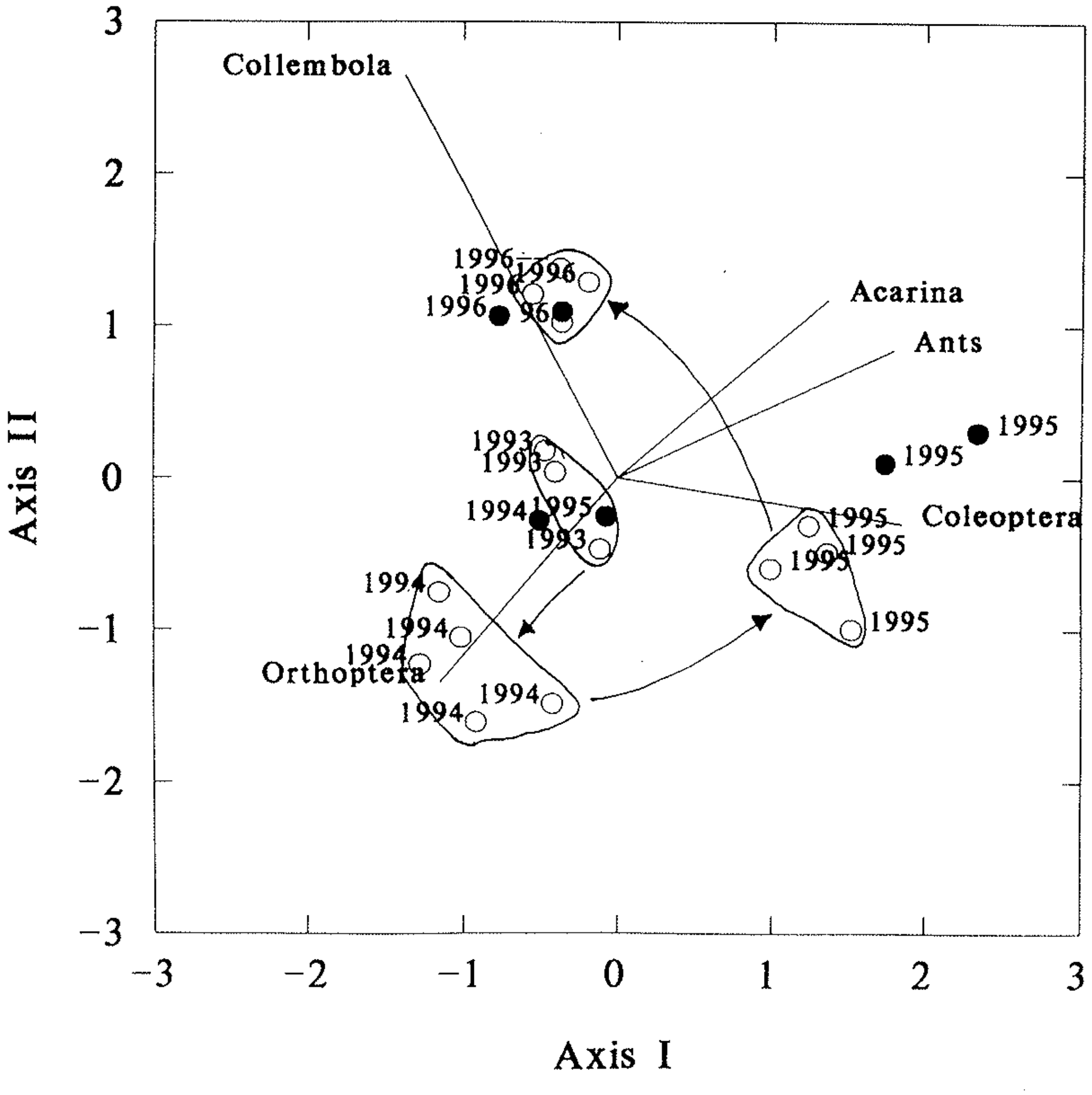


Fig.14. Principal Components Biplots comparing relative abundance in spring of unburnt sites with burnt sites by year of sample. Open squares = unburnt sites; filled squares = autumn 1993, spring 1994 & autumn 1996 burnt sites. Numeric labels indicate year of sample.

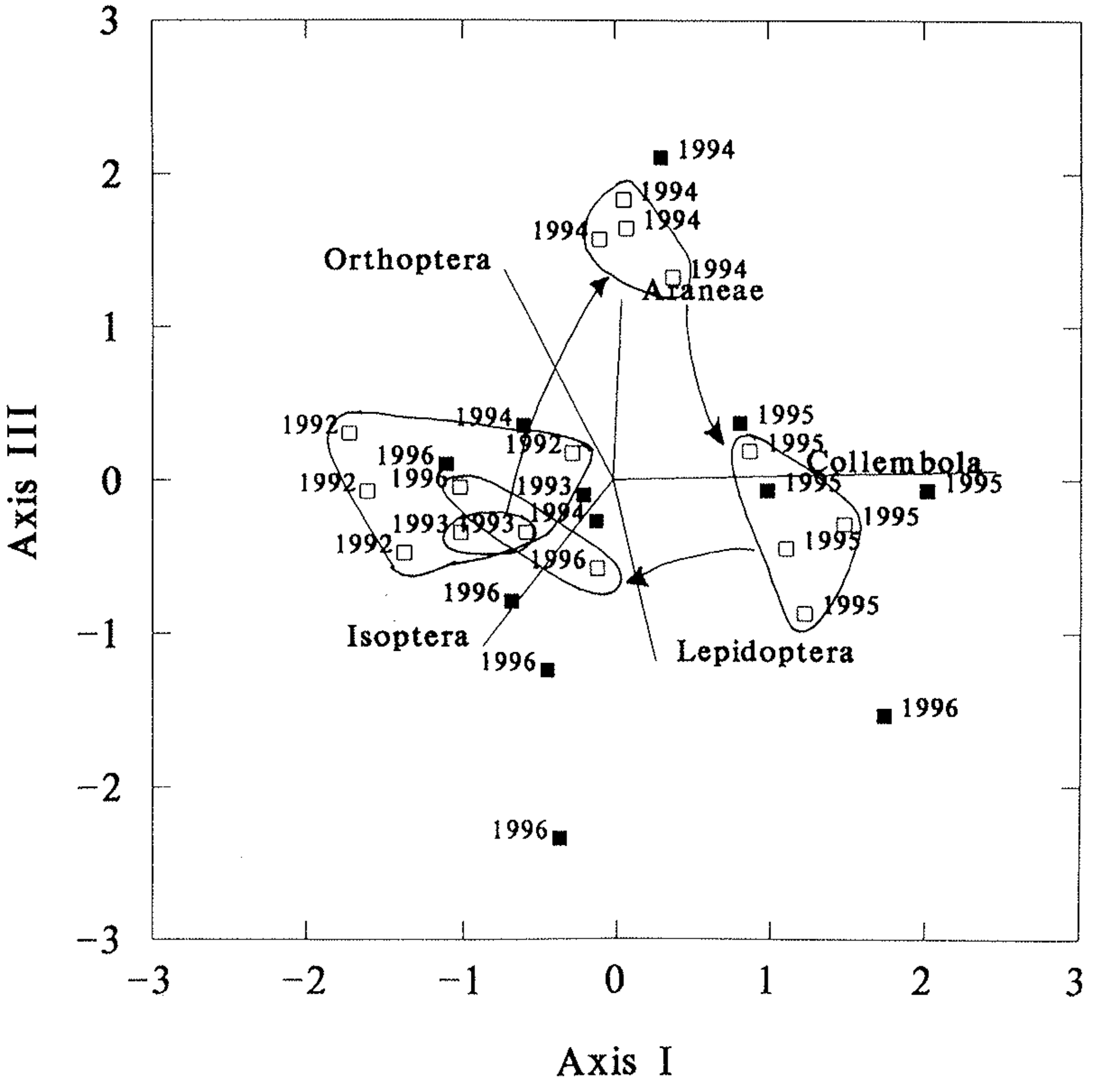
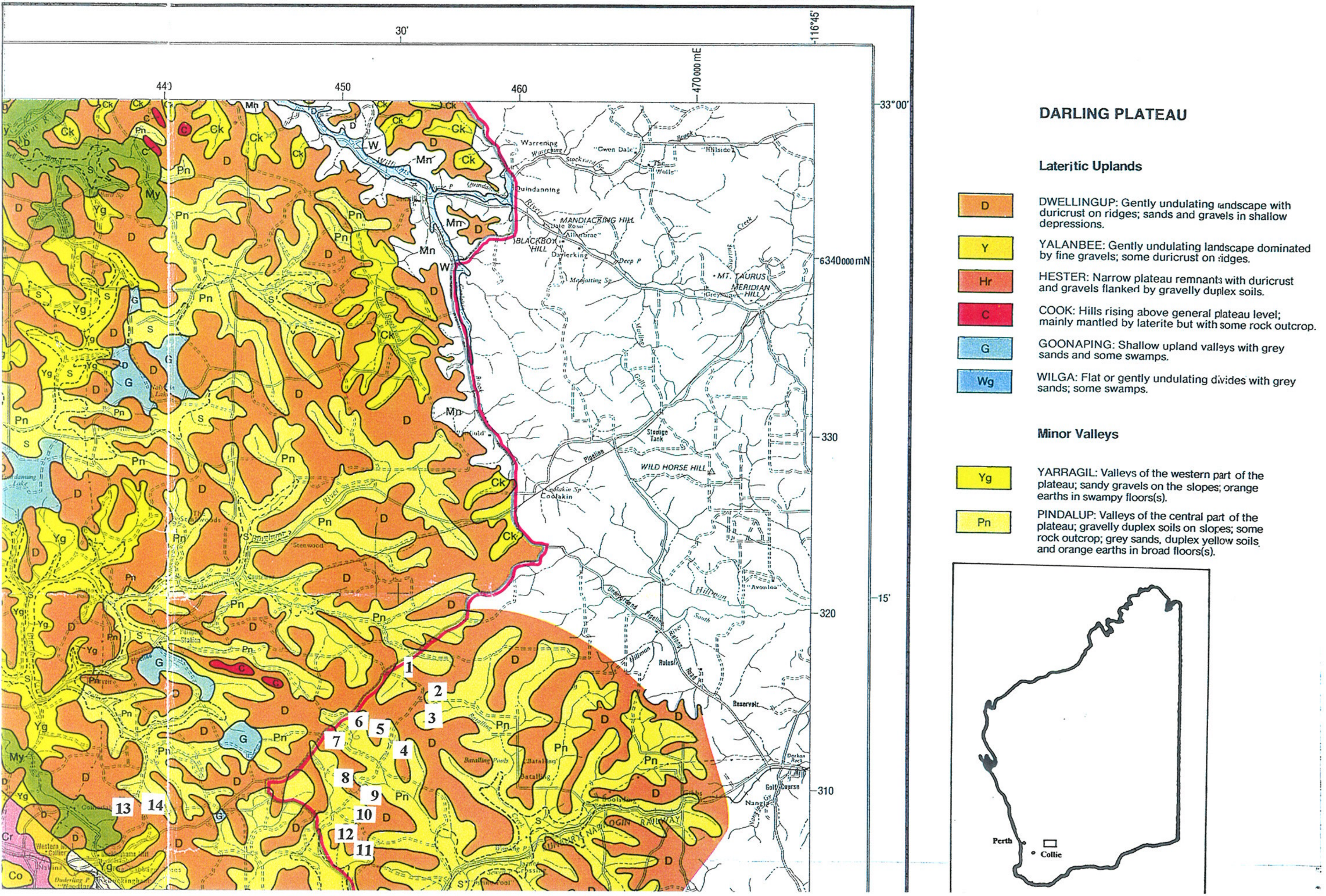


Fig.1. Study area and landforms. (Adapted from Briggs et. al. 1980). COLLIE SHEET



DARLING PLATEAU

Lateritic Uplands

D	DWELLINGUP: Gently undulating landscape with duricrust on ridges; sands and gravels in shallow depressions.
Y	YALANBEE: Gently undulating landscape dominated by fine gravels; some duricrust on ridges.
Hr	HESTER: Narrow plateau remnants with duricrust and gravels flanked by gravelly duplex soils.
C	COOK: Hills rising above general plateau level; mainly mantled by laterite but with some rock outcrop.
G	GOONAPING: Shallow upland valleys with grey sands and some swamps.
Wg	WILGA: Flat or gently undulating divides with grey sands; some swamps.

Minor Valleys

Yg	YARRAGIL: Valleys of the western part of the plateau; sandy gravels on the slopes; orange earths in swampy floors(s).
Pn	PINDALUP: Valleys of the central part of the plateau; gravelly duplex soils on slopes; some rock outcrop; grey sands, duplex yellow soils and orange earths in broad floors(s).

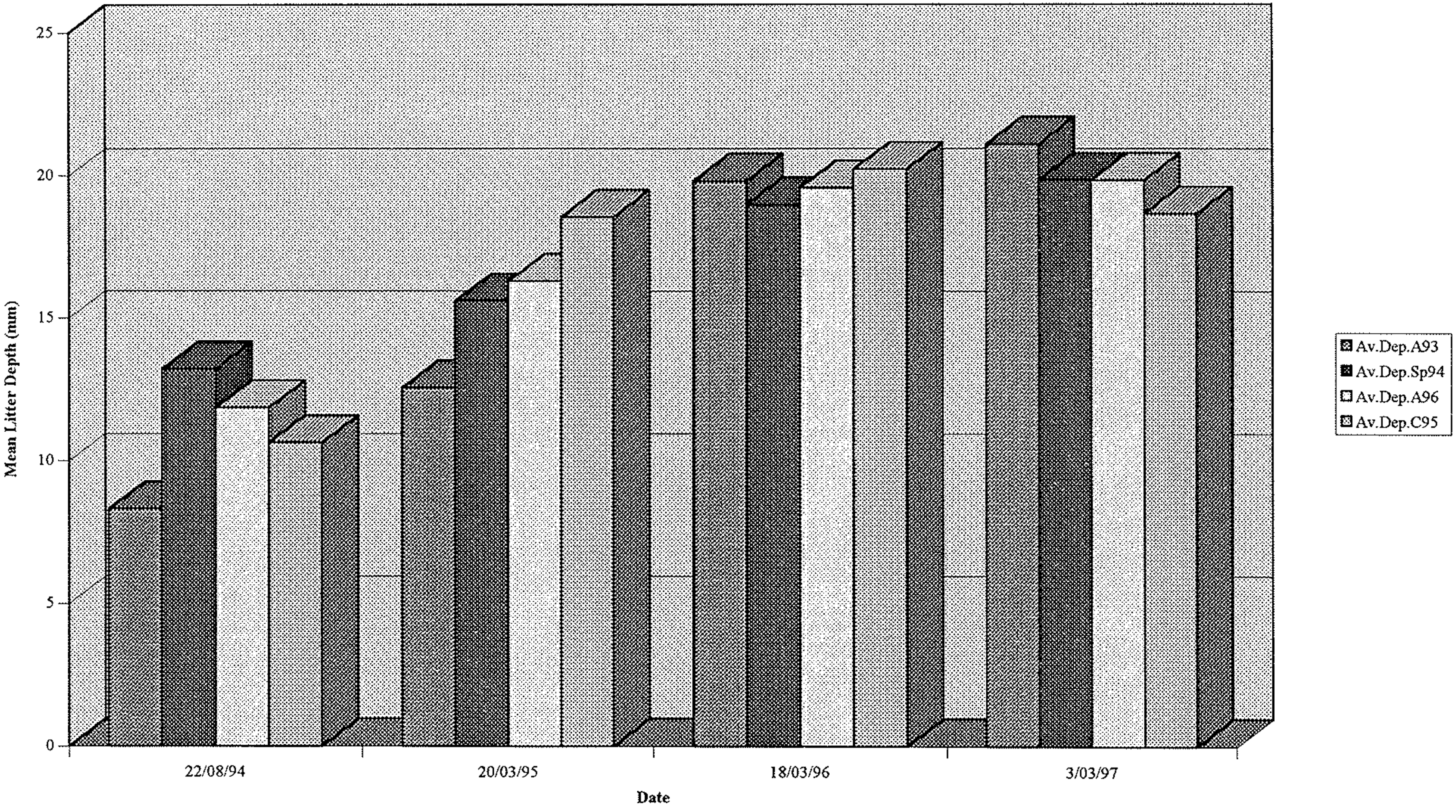


Fig.3: Mean Leaf Litter Depth at Unburnt Control Sites and Sites Burnt in Autumn 93, Spring 94 and Autumn 96.
Mean Litter Depth (mm)
25
20
15
10
5
0
22/08/94
20/03/95
18/03/96
3/03/97
Date
Av.Dep.A93
Av.Dep.Sp94
Av.Dep.A96
Av.Dep.C95

Fig.4: Median Leaf Litter Cover at Control Sites and Sites Burnt in Autumn 93, Spring 94 and Autumn 96.

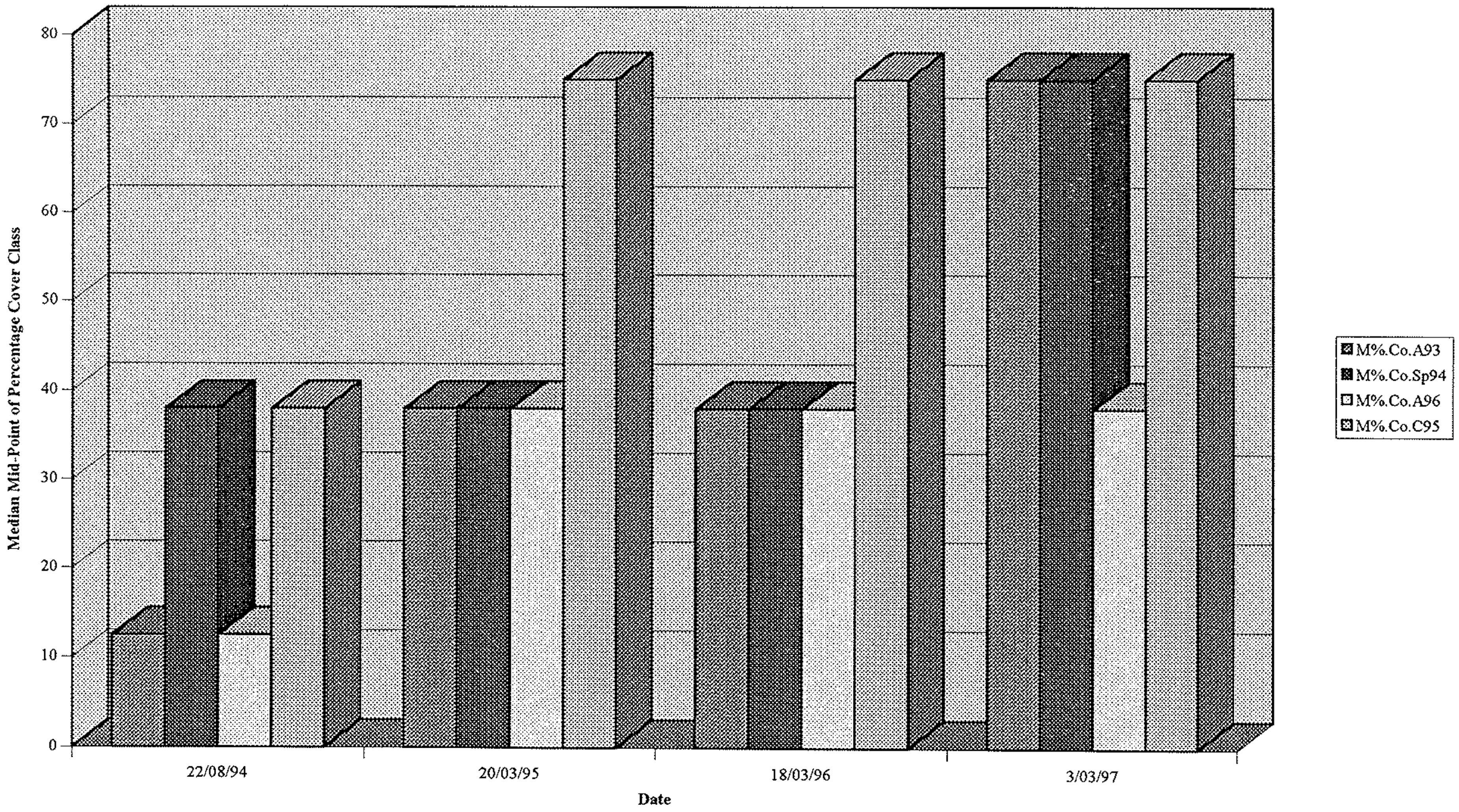
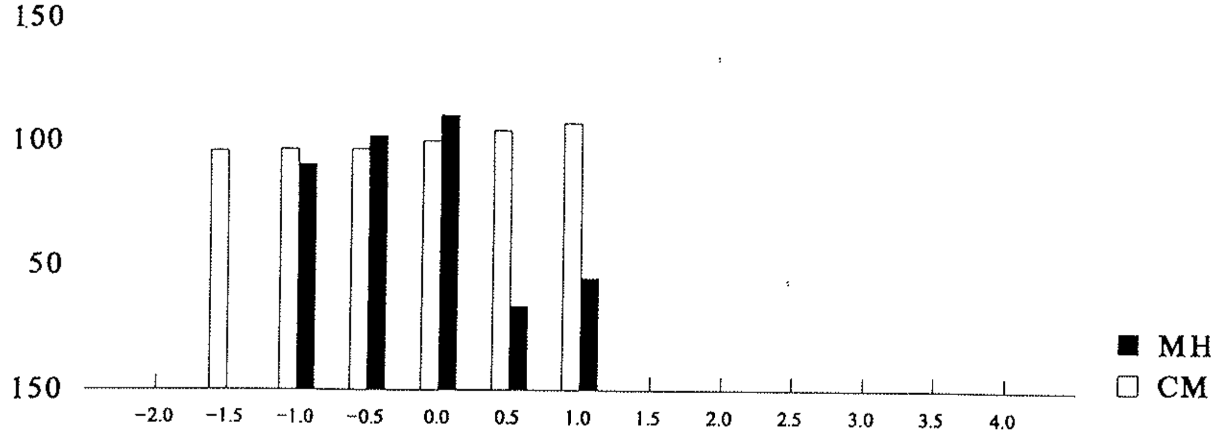
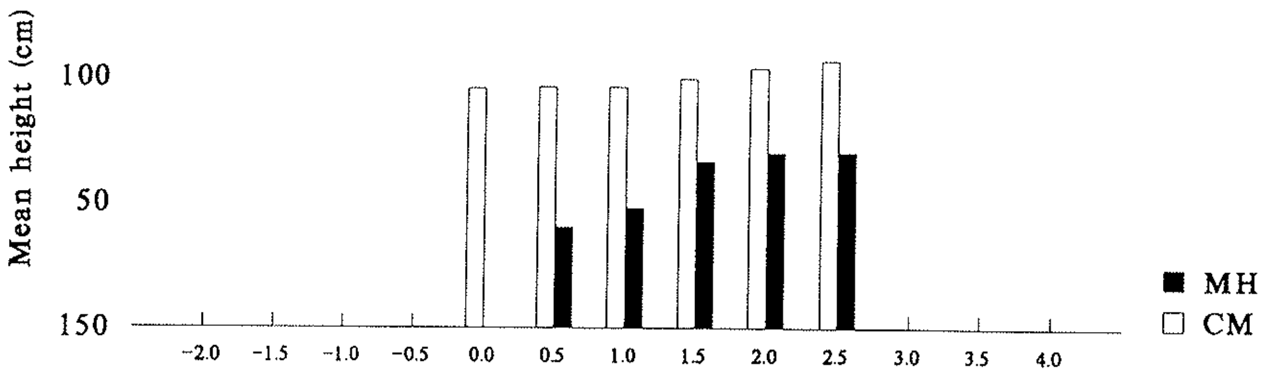


Fig.5 Mean Pooled Top Height of Dominant Shrubs at Unburnt Control Sites and Sites Burnt in Autumn 1993, Spring 94. CM: open columns are control means, HM: closed columns are burnt site means.

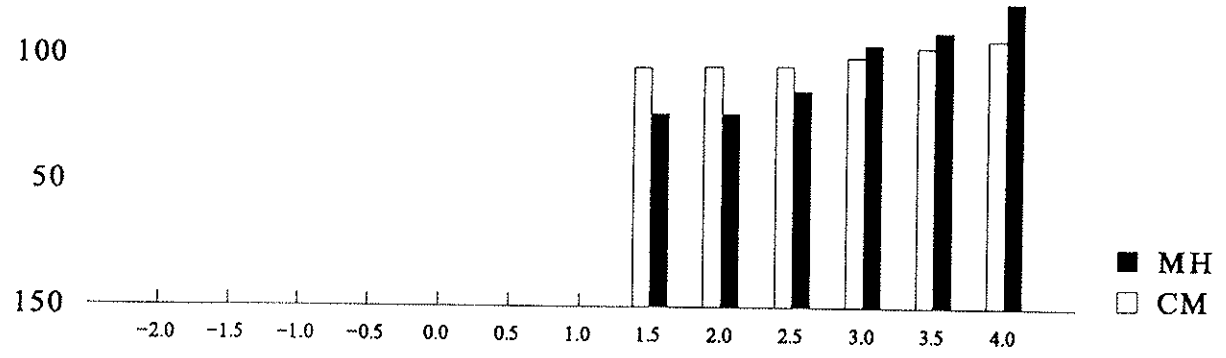
a) Autumn 1996 fires:



b) Spring 1994 fires:



c) Autumn 1993 fires:



d) All fires combined:

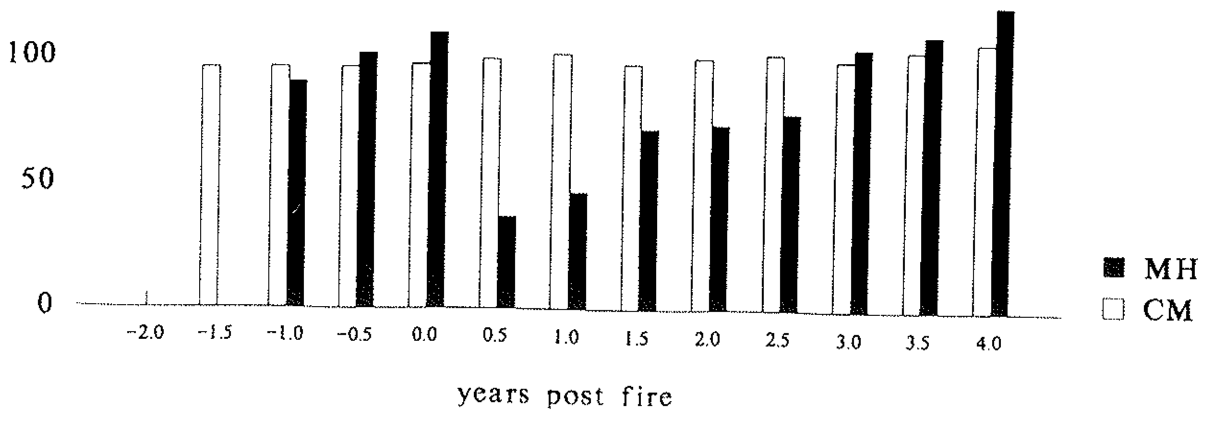


Fig.15. Principal Components Biplots comparing relative sample richness in spring of unburnt sites with burnt sites by year of sample. Open squares = unburnt sites; filled stars = high & low intensity spring 1994 burnt sites; filled diamonds = high intensity autumn 1993 & high & low intensity autumn 1996 burnt sites. Labels indicate year of sample.

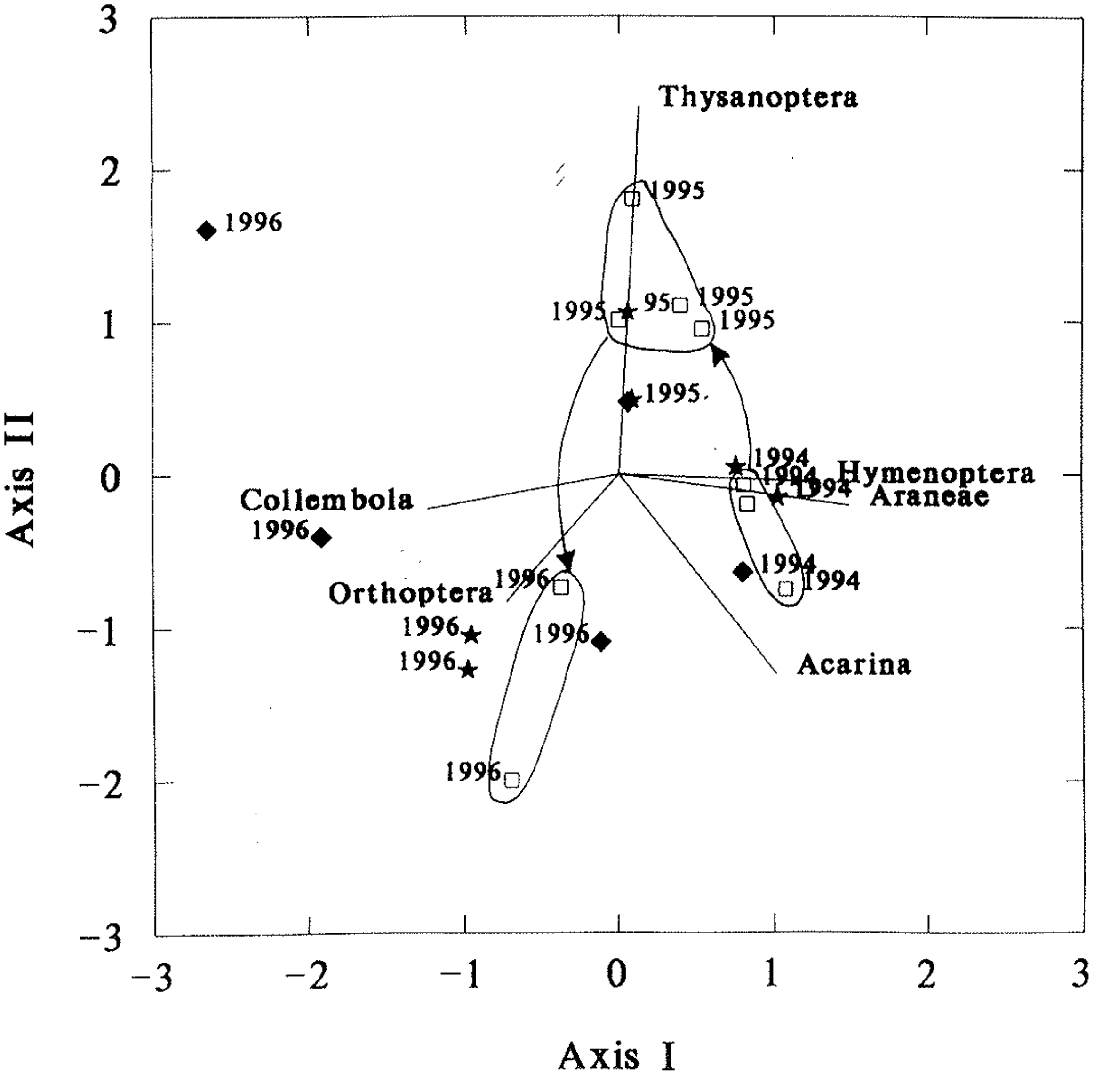


Fig.16. Principal Components Biplots comparing relative sample richness in autumn of unburnt sites with burnt sites by year of sample. Open circles = unburnt sites; filled circles = high intensity autumn 1993 & high & low intensity spring 1994 burnt sites. Labels indicate year of sample.

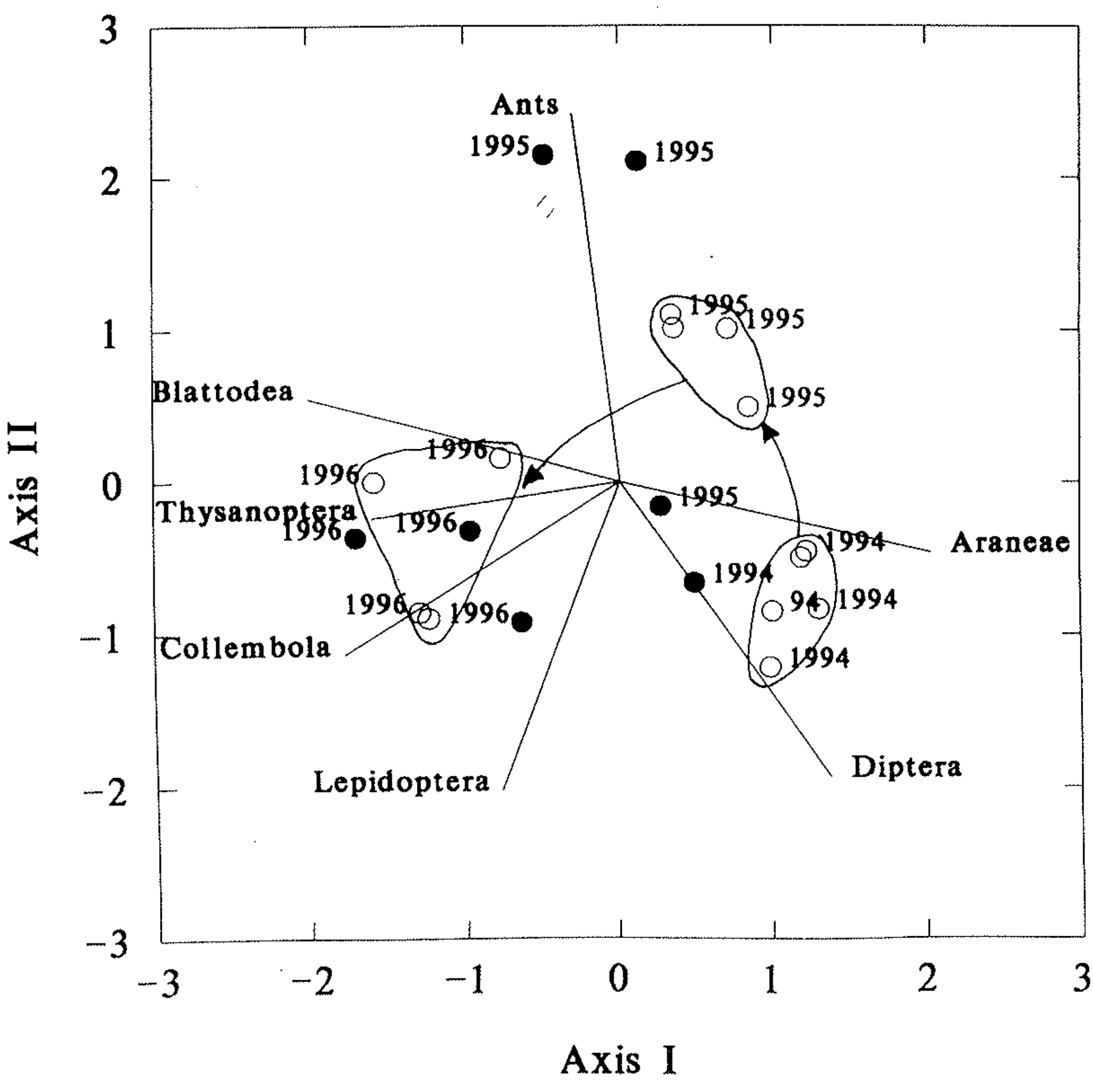


Fig.17: The Size Frequency of Trophic Guilds of Litter Beetle Morphospecies by Body Length

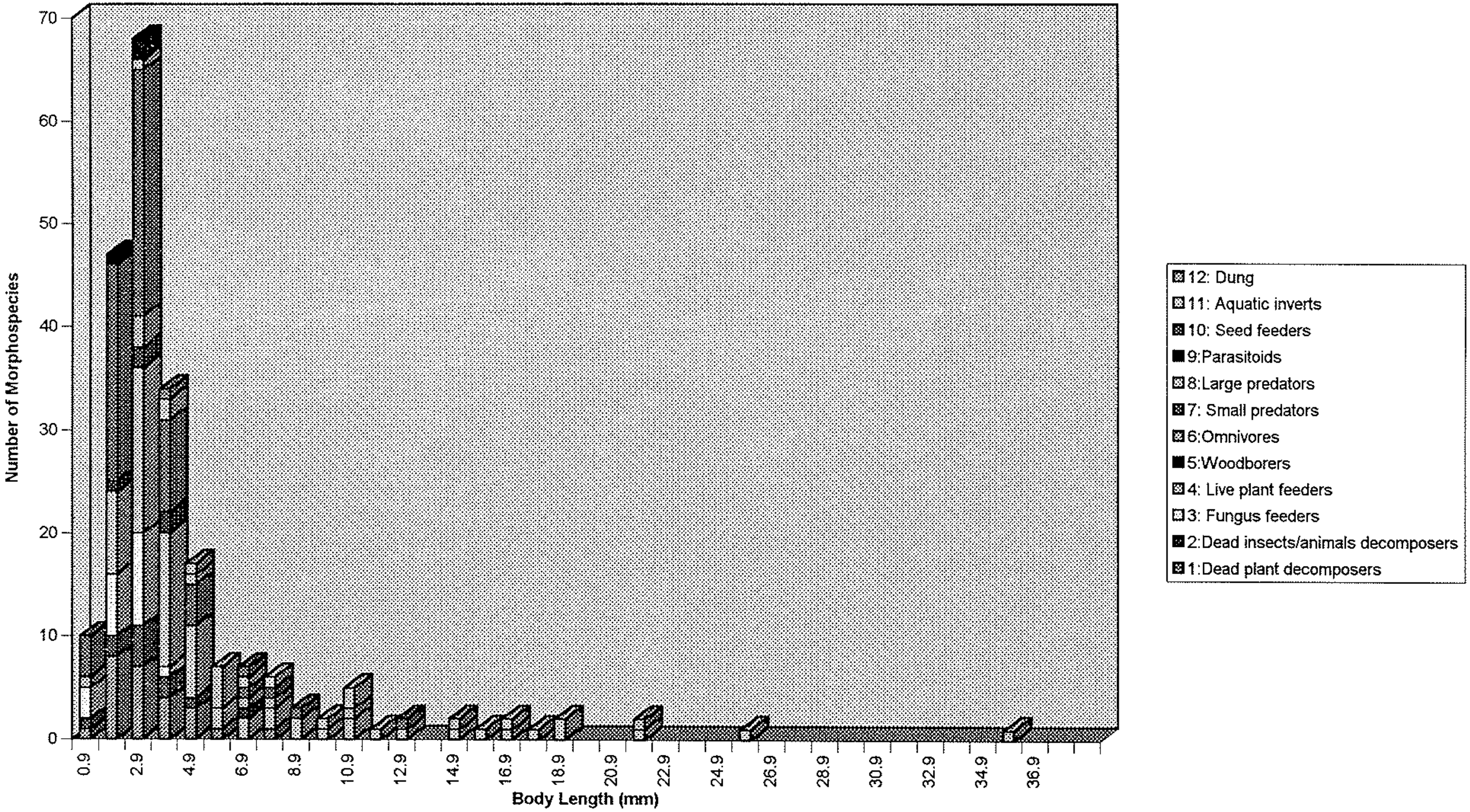


Fig.18: Relative Mean Volume of Beetle MorphospeciesTrophic Guilds at Unburnt Control Sites.

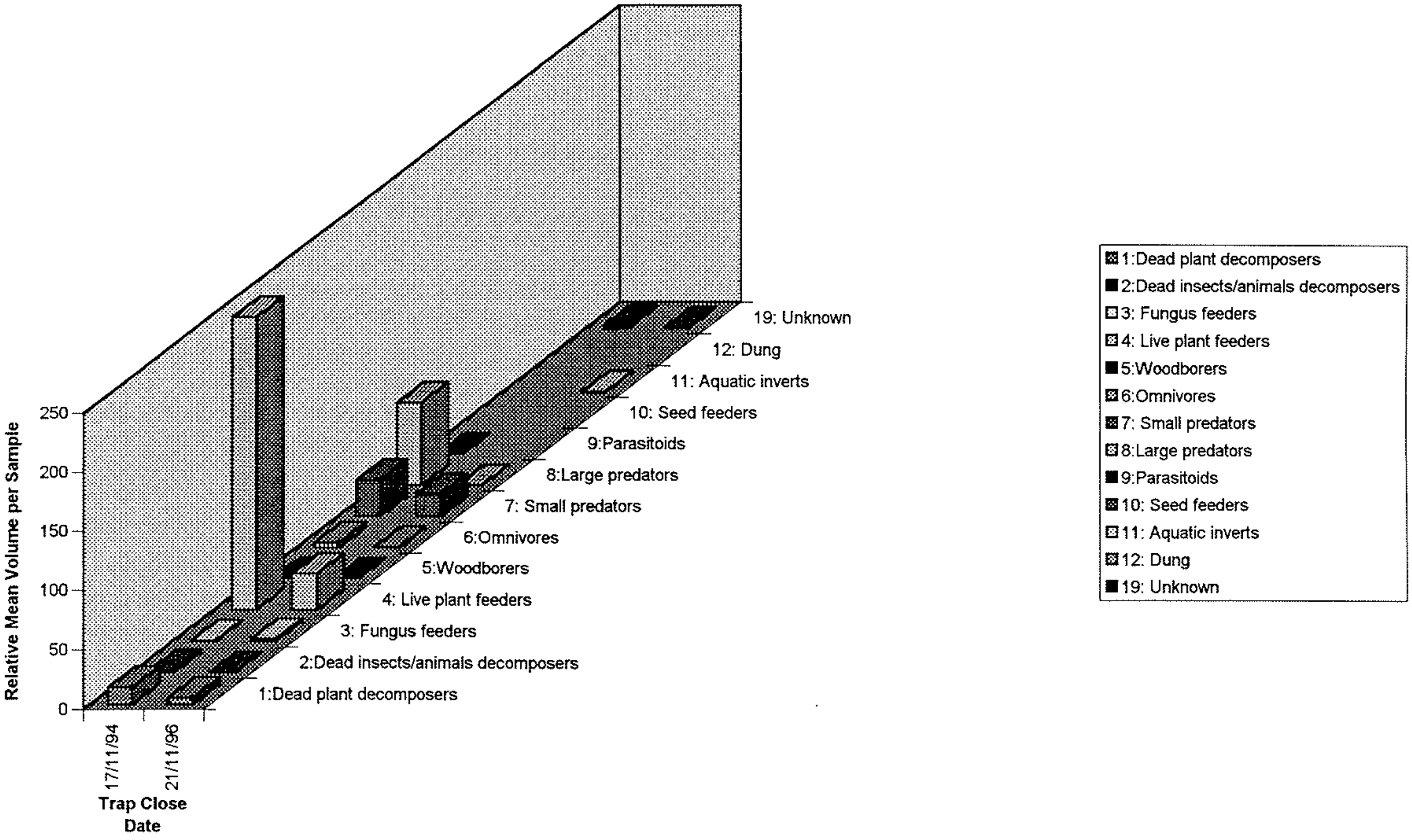


Fig.19: Relative Mean Volume of Beetle Trophic Guilds at Sites Burnt in Autumn 1993.

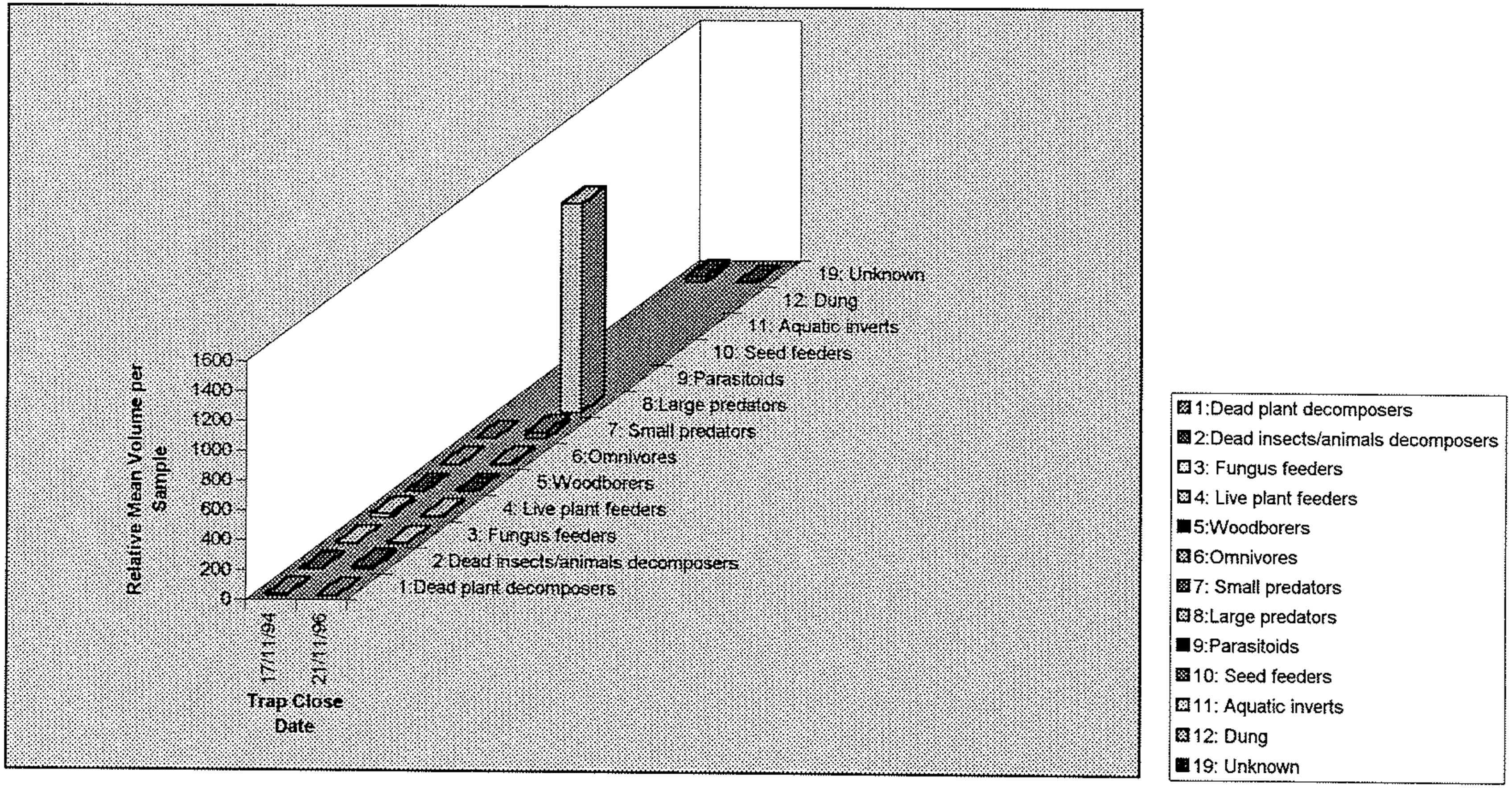


Fig.20: Relative Mean Volume of Beetle Morphospecies Trophic Guilds at Sites Burnt in Spring 1994.