Saproxylic beetles associated with habitat features in *Eucalyptus obliqua* trees in the wet eucalypt forests of southern Tasmania

by

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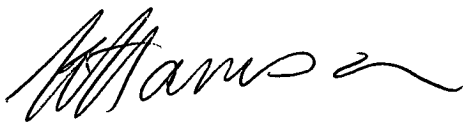
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Abstract

Old, larger-diameter eucalypt trees are a common structural feature of mature, unharvested wet forests in temperate Australia. In Tasmanian production forest, such trees will become rarer since there is insufficient time under the current prescribed rotation length of 80-100 years for replacements to regrow following clearfelling. Drawing on insights from overseas studies, one question that arises is what effect this anticipated change in age structure may have on tree-dependent biodiversity. In Tasmania, the relationships between tree age and saproxylic organisms (dead wood dependent) are insufficiently understood to allow explicit consideration of either their role as 'ecosystem engineers' (e.g. in hollow formation) or their conservation requirements in production forest landscapes. This thesis seeks to redress this deficiency. It documents two main studies that together represent the first attempt to quantify the saproxylic beetle fauna of living *Eucalyptus obliqua* trees - the dominant wet eucalypt species in Tasmania.

The first study investigated the saproxylic beetle fauna of young (69 years old), medium-aged (105 years old) and old (>150 years old) *E. obliqua* trees. Beetle associations with different aged trees and different wood fractions (stem, branches and bark) were explored by emergence trapping of wood fractions from six trees in each of the three age classes. The habitat within the stems of trees from each of the three age-classes was investigated by destructive sampling of wood billets. Wood within the stem was classified into eleven rotten wood types.

Trees in the oldest age-class were found to support a richer and more distinctive saproxylic beetle fauna compared to those in the two younger age-classes. They had higher overall species richness per tree and per surface area sampled; higher richness of obligate saproxylic beetle species; and a different assemblage composition of obligate saproxylic beetle species compared to trees in the younger age-classes. By comparison, trees in the two younger age-classes shared similar species richness and composition.

Stem-dwellers accounted for much of the distinctiveness of the saproxylic beetle fauna of trees in the oldest age-class. This may have been due to the more complex array of habitats present in the stems of these old trees compared to stems of trees in the two younger age-classes. Trees in the oldest age-class harboured more rotten

wood types and a larger proportion of decayed stem compared to the two younger age-classes. A strong correlation was found between the assemblage composition of obligately saproxylic beetles and the assemblage composition of rotten wood types present within a tree. Specific associations with particular rotten wood types were found for several beetle species.

Eucalyptus obliqua wet forests are naturally fire-prone and likely to harbour beetle species which are adapted to this disturbance, and which may count as 'ecosystem engineers' if they then facilitate the creation of more complex habitat features (such as tree hollows) that are utilised by various species including arboreal mammals and birds. Thus the second study was a manipulative experiment examining the role of saproxylic beetles in habitat formation in trees, and their association with fire-wounds and mechanical wounds..

Beetle associations were assessed by capturing (a) beetles attracted to newly created mechanical wounds and fire-wounds (sticky trapping), and (b) beetles that colonised these same wounds (emergence trapping a year later), on 45 trees (fifteen trees from each treatment: wound, burn, and control).

Preferences for burnt over unburnt recently exposed sapwood were identified in seven saproxylic beetle species. Several further species with the potential to act as 'ecosystem engineers' in ageing *E. obliqua* trees were identified through comparing findings from the two studies.

On the basis of the findings from these studies, management recommendations are made that, if implemented, would demonstrate a more pre-emptive approach to saproxylic biodiversity conservation in production forests. In general, efforts should be made to ensure that long-term structural complexity is enhanced beyond levels which will eventuate under the current silvicultural practices. This could be achieved by introducing variability in harvesting intensity and mature tree retention levels, in rotation length and in coupe size. Additionally, where the forest landscape is currently dominated by younger managed stands, 'ecological thinning' could be considered as a means of accelerating the development of structurally more complex forest. At the landscape level, management planning should consider maintaining sufficient spatial connectivity and temporal continuity of a range of tree age-classes to ensure the maintenance of the dependent fauna.

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Chapter 1

General Introduction

1.1 INTRODUCTION

This thesis investigates saproxylic beetles associated with living *Eucalyptus obliqua* in the southern wet eucalypt forest of Tasmania, Australia. In better-studied and longer-managed northern temperate forests, saproxylic (dead wood dependent) organisms (for instance many beetles) are of particular conservation concern because of their dependence on a habitat largely present in, or derived from, old trees. In Tasmania, the disturbance dynamics are somewhat different, and there is a shorter history of intensive forestry and of scientific research. Hence, the taxonomy of this fauna and its role in ecological processes within living eucalypts is insufficiently understood. A goal of modern sustainable forestry is the conservation of native biodiversity; to be able to effectively achieve this requires an understanding of the fauna and the likely impact of forestry operations. This introductory chapter provides a background to the study of saproxylic beetles and Tasmanian forest management, by presenting what is already known from studies conducted in Tasmanian and other forest ecosystems and how this relates to the wet eucalypt forests of Tasmania.

What are saproxylic invertebrates and why are they important?

Saproxylic invertebrates are those "that depend, during some part of their lifecycle, upon dead or dying wood of moribund or dead trees (standing or fallen), or upon wood-inhabiting fungi; or upon the presence of other saproxylics" (Speight 1989). A broad range of invertebrate taxa are known to be saproxylic and include representatives from all major insect orders (Alexander 2002; Dajoz 2000; Kirby and Drake 1993; Speight 1989). Whilst the majority of saproxylic species can be found within the orders Coleoptera (beetles) and Diptera (flies), many species can also be found in the non-insect groups: for instance, mites, pseudoscorpions and onychophorans. Saproxylic beetles were chosen for this study as they have a broad taxonomic and functional diversity, and because their ecology is well-understood and their identification is generally achievable in comparison to other taxa.

Saproxylic species are an extremely speciose functional group found in native forests throughout the world (Grove 2002c). From a single forest in Finland, 287 species of saproxylic beetles were recorded (Hanski and Hammond 1995) and a similar number of species (257 species) were recorded from dead aspens in one Canadian forest (Hammond 1997). Tasmanian wet eucalypt forests appear to harbour a remarkably high degree of saproxylic beetle diversity compared to other regions (reviewed in Grove (2002c)). A total of 539 saproxylic beetles have been found in the Warra Long Term Ecological Research Site (LTER) in Tasmania's southern forests (Grove, SJ pers. comm.), a number which includes 350 species that were collected from only 104 *E. obliqua* logs (Yee 2005).

Saproxylic invertebrates are an integral component of a forest ecosystem. They can play an important role in the decomposition of woody material (which is central to nutrient cycling) by assisting the action of fungi and micro-organisms (Hanula 1993; Schowalter *et al.* 1998; Swift and Boddy 1984). Saproxylic species may also be important in other ecological processes such as hollow formation where they can act as 'ecosystem engineers' (Adkins 2006; Mackowski 1987). Hollow formation can be aided by primary colonising saproxylic species such as wood-boring beetles which have the ability to create entrance points into the heartwood and facilitate the spread of other decomposer organisms with a tree (Boddy 2001; Elliott and Bashford 1984; Elliott and de Little 1984; Käärik 1975; Käärik 1974; Perry *et al.* 1985; Speight 1989). Their role may be even more important in Australia than elsewhere, as few vertebrate species are capable of excavating hollows, so the hollow-creation process is more dependent on the action of other agents such as wood-decay fungi, fire and wood-boring invertebrates (Adkins 2006; Gibbons 1994; Inions *et al.* 1989; Mackowski 1987; Whitford 2002).

Saproxylic fauna (particularly beetles) are reasonably well known in some regions of the world. The United Kingdom and Fennoscandia have the best documented saproxylic fauna, with other areas of Northern Europe not far behind. This can be attributed in part to a traditionally high level of interest in natural history (the fauna was documented in Sweden by Palm (1959) and in the UK by Elton (1966)) and a long history of forest use highlighting conservation issues facing saproxylic species. In both of these regions the ecology, rarity and degree of threat to many saproxylic species has been collated (United Kingdom: Alexander (2002), Shirt (1987); and

Sweden: Gärdenfors (2000)). The awareness of saproxylic invertebrates and potential impacts from forest use has started to increase in other regions, such as North America (Hammond 1997; Hammond *et al.* 2001, 2004; Hanula 1993; Spence *et al.* 1996).

Until recently, few studies have investigated the saproxylic invertebrate fauna of Australia. The majority of research on invertebrates associated with eucalypt ecosystems has focussed on canopy- or ground-dwelling species (Majer *et al.* 1997). Previously the main emphasis of the limited number of studies examining saproxylic species has been on their role as pests or as potential pests (Elliott and Bashford 1984; Elliott and de Little 1984). In more recent times, the Australian saproxylic invertebrate fauna has received a little more attention, with a few studies been conducted in Tasmania and Northern Queensland investigating the potential impacts of forestry operations on this fauna (e.g. Bashford *et al.* 2001; Grove 2002a, 2002b; Grove *et al.* 2002; Meggs and Munks 2003; Michaels and Bornemissza 1999; Yee 2005; Yee *et al.* 2001). The studies by Michaels, Bornemissza and Meggs have focused on a specific group of beetles (log-dwelling lucanids), while the studies conducted by Yee, Grove and Bashford have investigated a larger range of the saproxylic fauna.

Wet eucalypt forests and the impact of forestry

Wet eucalypt forests are ecologically and economically important to Tasmania (Whiteley 1999) and encompass an area of 883 000 ha, chiefly in the south-west and north-west of the state (Forestry Tasmania 1998b). Wet eucalypt forest comprises two broad forest types; wet sclerophyll (eucalypt canopy with an understorey of broad-leaved shrubs or ferns) and mixed forest (eucalypt canopy with rainforest elements in the understorey) (Kirkpatrick *et al.* 1988).

Eucalyptus obliqua wet eucalypt forest is the most widespread forest type and is naturally fire-prone, with wildfires the main large-scale disturbance event. Wildfires occur at varying frequencies ranging from 20 to 400 years (Alcorn *et al.* 2001; Hickey *et al.* 1998) and are thought to be central to maintaining the dynamic wet eucalypt forest-rainforest boundaries in Tasmania (Jackson 1968). Wildfires in Tasmanian wet eucalypt forest, unlike in other wet eucalypt areas of Australia, are

less frequently stand-replacing in intensity, due to the cool, moist climate (Grove *et al.* 2002). This has lead to much of the southern wet eucalypt forest being a mosaic of structurally complex multi-aged forest, with patches of single-age forest (Hickey *et al.* 1998). The Tasmanian eucalypt forests have been noted for their high level of biodiversity and regional endemism (Norton and May 1994; Recher *et al.* 1996), which is likely to be partly related to the high level of structural diversity within these forests (Butler *et al.* 2002; Cork and Catling 1996; Franklin *et al.* 2002; Grove 2002b; McComb and Lindenmayer 1999; Scotts 1994).

Since European settlement (1788), rapid, fundamental change has occurred in a large proportion of Australia's eucalypt forests (Norton and May 1994), with approximately half of Australia's forest having been cleared or severely altered (Young *et al.* 1990). Human-induced change of forests for agricultural production, forestry, mining, urbanisation, transport and recreation has lead to the current level of forest cover (Norton 1997; Norton and May 1994). In 1997 the Tasmanian Regional Forest Agreement was invoked to ensure the long-term sustainable management of Tasmania's forests. This agreement sought to protect a minimum of 15% of the pre-1750 distribution of each forest ecosystem by incorporation into the Comprehensive Adequate and Representative (CAR) reserve system.

In the bioregion of this study (Southern Ranges Bioregion) around 35% (115, 200 ha) of the pre-1750 wet eucalypt forest lies within the CAR reserve system (CARSAG 2002). The CAR bioregions were classified largely based on vascular plant communities and the degree to which the adequacy of the vegetative communities coincide with communities of other species (such as saproxylic beetles) has not been sufficiently assessed (Grove *et al.* 2002; Yee 2005). Additional factors such as climate changes, potentially small range size of many Tasmanian saproxylic species and the possibility of large-scale wildfires suggest that a precautionary approach combining off-reserve conservation as well and on-reserve conservation would increase the likelihood of achieving the goal of sustainable forest management (Grove *et al.* 2002). The standard harvesting and regeneration technique in Tasmanian wet eucalypt forest is clearfelling, burning and broadcast sowing (CBS) (Forestry Tasmania 1998a), with a nominal rotation length of 80-100 years. This silvicultural regime was adopted as it was felt to somewhat mimic natural disturbance (wildfire) while also maximising the yield and

regeneration of timber trees (Attiwill 1994). However, the natural disturbance regime of a forest and forestry operations will never exactly match, as the basic principle of forestry is to remove timber from the forest (Haila et al 1994). Baker 2004 (and references therein) presents a comparison of wildfire and clearfelling silvicultural regimes. She identified the most crucial differences between CBS and wildfire to be the lowering of the stand age, due to a rotation length shorter (prescribed 80-100 yrs) than natural disturbance (variable 20-400 years); and the simplification of the overall stand structure due the reliance on single-aged stands rather than multi-aged stands which are indicative of a typical natural disturbance regime. CBS silviculture also retains fewer structural elements (such as live fire-damage trees and fire-killed standing trees) than a wildfire. A younger stand, due to a silvicultural rotation more frequent than the occurrence of natural disturbance events, means that forest characteristics and structures typical of biologically old forests (such as over-mature trees, snags and large diameter CWD) will not have time to develop (Lindenmayer *et al.* 2000; Lindenmayer and Franklin 1997; Niemelä 1999). Each successive rotation will further decrease the level of these old-growth features within the stand. Large diameter coarse woody debris (CWD) will generally be present after the first rotation, but as these logs decompose there will be no old large-diameter trees to create new inputs of this larger diameter wood.

As well as the differences between CBS and natural disturbances from wildfire at the stand-level, there are the landscape-level changes. The spatial and temporal dynamics of a forest created by CBS differ from those created by a wildfire (Lindenmayer *et al.* 1990; Niemelä 1999). Fire generally covers a far larger area (1000's of hectares) than CBS (stands generally 50-100 ha), but within the affected forest, the structure is more complex than CBS, due to differing levels of fire intensity (Baker *et al.* 2004; Lindenmayer *et al.* 1990).

The impact of CBS silviculture on the long-term availability of CWD in Tasmania's wet eucalypt forests has been modelled using a rotation length of 100 years and compared with 'natural' wildfire disturbance (Grove *et al.* 2002). Many parameters (such as log decomposition rates and volume of CWD in various decomposition stages) were unknown, and further studies e.g. Stamm (2006) have refined the initial model. These models have projected that successive CBS logging cycles will significantly reduce the amount and complexity (less range in sizes) of CWD within

the stand compared to natural inputs from wildfire. These differences become even more apparent if the stand is converted to plantation after logging or if fuel-wood harvesting is practised.

What impact is CBS silviculture likely to have on saproxylic invertebrates in wet eucalypt forests?

Saproxylic invertebrates are by definition dependent on dead wood, therefore any silvicultural regime that alters this aspect of the forest ecosystem will, to varying degrees, impact upon them. The majority of research into the effects of forestry (and other human induced changes in the landscape) on saproxylic invertebrates comes from the United Kingdom and Northern Europe, where a long history of deforestation and intensive forest management has lead to many saproxylic species being considered threatened (Berg *et al.* 1995; Hammond and Harding 1991; Jonsell 1999; Jonsell *et al.* 1998; Key and Ball 1993; Kirby and Drake 1993; Speight 1989; Sverdrup-Thygeson and Ims 2002). Habitat loss has occurred at many scales, from large areas of native forest altered for agriculture, urbanisation and non-native plantation, to the loss of specific habitats (such as CWD, large-diameter old trees or burnt substrates) within managed native forests. The significant impact this has had on saproxylic communities has been recognised and a suite of research projects have been conducted in order to establish what their ecological requirements are and how best to alter current forest (and other land-use) practices to reduce the negative impacts on saproxylic species.

These studies (mainly from Northern Europe) have found saproxylic invertebrates to have a wide range of habitat requirements and differing degrees of habitat specificity. Associations have been found with many different microhabitats provided by trees and dead wood. These include:

- Wood type (e.g. veteran living tree, standing dead tree (snag), downed branch or log (fine and coarse woody debris)) (Jonsell *et al.* 1998; Ranius 2002; Schiegg 2001; Singh and Bhandari 1997);

- Wood size (large or small diameter) or age (Esaki 1996; Grove 2002b; Hammond *et al.* 2004; Jonsell *et al.* 1998; Meggs 1996; Schiegg 2001; Siitonen and Saaristo 2000; Yee 2005);

- Location (degree of sun or shade) (Ahnlund 1996; Kaila *et al.* 1997; Lindhe *et al.* 2005; Martikainen 2001; Økland *et al.* 1996; Ranius and Jansson 2000; Sverdrup-Thygeson and Ims 2002) and orientation (vertical/horizontal) (Jonsell *et al.* 2004; Jonsell and Weslien 2003; Nilsson and Baranowski 1997);

- Tree genus (Bakke 1999; Irmler *et al.* 1996; Kappes and Topp 2004; Kohler 2000);

- Decay stage (Dajoz 2000; Hammond *et al.* 2001; Irmler *et al.* 1996), decay type (Araya 1993; Meggs 1996) and fungal flora (Jonsell *et al.* 2005; Kaila *et al.* 1994);

- Exposure to fire (Bohman 2004; Wikars 2002).

While these factors have been listed separately above, within a forest system they are all interrelated and it is a combination of factors that influences saproxylic beetle communities. Any reduction in the availability of any of these habitats by the modification of forest structure by production forestry has been linked with changes in saproxylic communities and the decline in the range and population of some species. Unmanaged forests have higher structural complexity than production forests, with features such as standing or fallen dead wood (particularly larger diameter), and old (over-mature) living trees commonplace; and generally provide many of the diverse habitat types utilised by different saproxylic species.

Two other important factors that influence structural complexity and are therefore linked with saproxylic invertebrate diversity are prior forest history (forest age, disturbance type and intensity)(Bakke 1999), and the degree of temporal and spatial connectivity (Harding and Alexander 1994; Kohler 2000; Schiegg 2000a, 2000b). Saproxylic fauna have been found to vary in relation to forest successional age. Hammond (2004) found a succession of saproxylic beetles inhabiting *Populus spp.* logs and snags in aspen in native boreal forests of different stand ages. Many saproxylic beetle species were found exclusively (or in greater abundance) in old stands or logs with large diameters; and the overall level of diversity was linked to the availability of wood in a wide range of decay stages.

The type and intensity of disturbance will alter the availability of some habitats and diversity of saproxylic species. In a Finnish study, forests containing more CWD

supported a greater diversity of beetle species than did forests where CWD was scarce due to removal during forest harvesting (Siitonen *et al.* 2000). Schiegg (2000a; 2000b) found that high dead-wood connectivity (distance between stands and within a forest the distance between dead wood pieces) must be achieved in managed forests to sustain species which are particularly vulnerable to fragmentation. This connectivity needs to be maintained both spatially and temporally, and the optimum arrangement will depend on the dispersal abilities of the relevant species. Saproxylic invertebrates have a variety of dispersal abilities, which may affect their success in coping with habitat loss or forest fragmentation (Jonsell 1999; Jonsson *et al.* 2001; Ranius 2006; Rukke and Midtgaard 1998). This is currently an important area of research in the issue of saproxylic invertebrate conservation (Ranius 2006).

In comparison to Northern Europe and North America we know little about our saproxylic fauna and their habitat requirements in Australia. It is reasonable to assume that our saproxylic fauna, like that in Northern Europe and Northern America, will have a broad range of habitat associations and requirements. The majority of Tasmanian studies have focused on the impact of forest harvesting on downed log (CWD) availability and potential threats from habitat loss on its associated fauna. Meggs (1996; 2003) as well as Michaels (1999), investigated obligate log-dwelling lucanids and their habitat requirements (ecology and biogeography). As a result of their studies, three stag beetle species (*Hoplogonus simsoni, Lissotes latidens* and *Lissotes menalcas*) have been officially listed as threatened under the Tasmanian 'Threatened Species Protection Act' (TSPA 1995). The impact of successive CBS cycles on *Lissotes menalcas* (Mt Mangana Stag Beetle) has been modelled (Grove *et al.* 2002) and indicates that under prescribed rotation lengths CBS silviculture will lead to a significant and permanent reduction in the habitat required within the logged stand (CWD).

Comprehensive studies of saproxylic beetles associated with large and small diameter *E. obliqua* logs in early (Bashford *et al.* 2001; Grove and Bashford 2003) and intermediate (Yee 2005) decomposition stages from the Warra region have been conducted. The study being conducted by Forestry Tasmania (Grove and Bashford 2003) has been designed as a long-term experiment investigating changes in saproxylic beetle fauna over time, from initial felling until final decomposition.

Yee (2005, 2006) found different beetle communities inhabiting small and large diameter logs. She also found different beetle communities in logs in mature versus logging-regenerated forests. This highlights the potential impact of CBS silviculture on saproxylic communities, as the current prescribed rotation length of 80-100 years will be shorter than the time needed for new trees to develop the larger diameter logs. The differences amongst saproxylic communities in the forest types may lessen over time as the young forest ages (the logging regenerated forest was younger (and more open) than the mature forest) (Yee 2005). However, the differences in communities may also be attributed to differing microhabitats within the mature unlogged forest (such as unburnt logs), that are not present in CBS regenerated forest.

Another key finding from Yee's (2005) study is that beetle species composition varied considerably over short geographical distances. This variation in beetle composition with distance has also been found in a study of ground-dwelling beetles in the Warra region (Baker *et al.* 2006). This has important implications for the adequacy of the current reserve system. As previously discussed the CAR forest reserve system is based on vascular plant communities, but the extent to which this correlates with communities of other species has not been sufficiently assessed. As the change in beetle communities are occurring within short geographical distances in one bioregion, it is likely that off-reserve conservation measures will be important in maintaining local species diversity.

What this study addresses

The few studies conducted on the saproxylic fauna of Tasmania's wet eucalypt forests indicate that our species, like that of Northern Europe and North America, have a complex range of habitat associations and any major changes in natural forest dynamics are likely to impact upon them. These impacts can be minimised by increasing our knowledge of the habitat requirements and dispersal ability of this fauna, so that forest managers can consider their requirements when determining silvicultural regimes; both within the stand and across the landscape.

The research presented within this thesis addresses some of the important gaps in our knowledge of the saproxylic fauna of Tasmanian wet eucalypt forests. It

investigates an earlier successional stage (living trees) than has been studied in the past; and, as well as providing knowledge on the fauna associated with living trees, it will assist in determining the degree of habitat specificity (e.g. logs and mature trees of different ages) within the fauna. Some degree of habitat specificity is likely, as many of the microhabitats found in the living tree are unique. In Sweden, old trees have been found to be a key habitat for 33 % of the 739 known threatened forest invertebrates (Berg *et al.* 1994).

The second component of this study explores the ecological role of saproxylic beetles in habitat creation, and investigates the role of wildfire within our forests for the maintenance of saproxylic beetle diversity. Within boreal forests wildfire suppression has been identified as one of the major alterations impacting on saproxylic species (Martikainen 2001; Økland *et al.* 1996; Wikars 1995, 2002). As the natural fire regime in Tasmanian wet eucalypt forests is not dissimilar to the natural fire regime of parts of the boreal forests, the Tasmanian saproxylic fauna is also likely to be influenced by the occurrence of wildfires.

1.2 THESIS OUTLINE

This thesis comprises two main studies: the first is a comprehensive investigation of saproxylic beetles inhabiting living *E. obliqua* in Tasmanian wet eucalypt forests and their specific habitat associations, the second is a manipulative study examining the role of saproxylic beetles in habitat formation, and their association with fire-created substrate.

The specific objectives of this thesis are:

- To document and describe the biology of saproxylic beetles inhabiting living *Eucalyptus obliqua* trees in the wet forests of southern Tasmania (Chapter 3).

- To evaluate mathematical techniques for the standardisation of sampling effort to allow the accurate comparison of species richness (Chapter 4).

- To compare saproxylic beetle assemblages found within living *E. obliqua* of different ages, and investigate their association with different tree fractions,

with particular consideration of increasing tree structural complexity on the composition of beetle communities (Chapter 5).

- To examine the relationship between saproxylic beetles, rotten wood type, wood decay fungi, and tree age in living *E. obliqua* (Chapter 6).

- To explore the role of saproxylic beetles in habitat formation and discover if species are responding to burnt substrate (Chapter 7).

- To discuss the habitat requirements of saproxylic beetles, and to examine the possible impacts of forest management and make recommendations for future research directions and forest management (Chapter 8).

Each chapter has been written in the format of a journal article or journal article in development but repetition between chapters has been kept to a minimum. Relationships between chapters are highlighted where appropriate. Study site descriptions and locations, as well as general sampling and statistical methods, are presented in Chapter 2.

Chapter 2

General Materials and Methods

2.1 STUDY SYSTEM

Wet eucalypt forests cover approximately 883 000 hectares of the 3.17 million hectares of native forest in Tasmania (National Forest Inventory 2005) and are classified into two broad forest types. These are wet sclerophyll (eucalypt canopy with an understorey of broad leaved shrubs or ferns) and mixed forest (eucalypt canopy with rainforest elements in the understorey) (Kirkpatrick *et al.* 1988). Three eucalypt species dominate Tasmanian lowland wet eucalypt forests: *Eucalyptus obliqua* L'Hérit., *E. regnans* F.Muell. and *E. delegatensis* R.T.Baker. Of these, *E. obliqua*-dominated wet forest is the most widespread. *E. obliqua* can reach ages of 400 years, reaching sizes of 75 m tall (Hickey *et al.* 2001) and well over 2 m girth (Alcorn *et al.* 2001). Over 48% of wet eucalypt forests are reserved, while the remainder are managed for a range of values including timber harvesting, water supply, conservation, recreation and environmental protection (National Forest Inventory 2005).

Wet eucalypt forest is an intermediate successional phase which is maintained by frequent large-scale wildfires (Jackson 1968). Wildfires occur at varying frequencies ranging from 20 to 400 years (Alcorn *et al.* 2001; Hickey *et al.* 1998). Managed lowland wet eucalypt forests are currently harvested by a silvicultural regime of clearfelling, burning and broadcast sowing (CBS) (Forestry Tasmania 1998a), with a nominal rotation length of 80-100 years.

2.2 STUDY AREA AND SITES

Two main studies were conducted as part of this thesis: an investigation of saproxylic beetles inhabiting living *E. obliqua*; and an examination of the role of saproxylic beetles in habitat formation. Both studies were located within the Warra Long Term Ecological Research (LTER) (Figure 2.1) in Tasmania's Southern ranges bioregion (Cofinas and Creighton 2001).
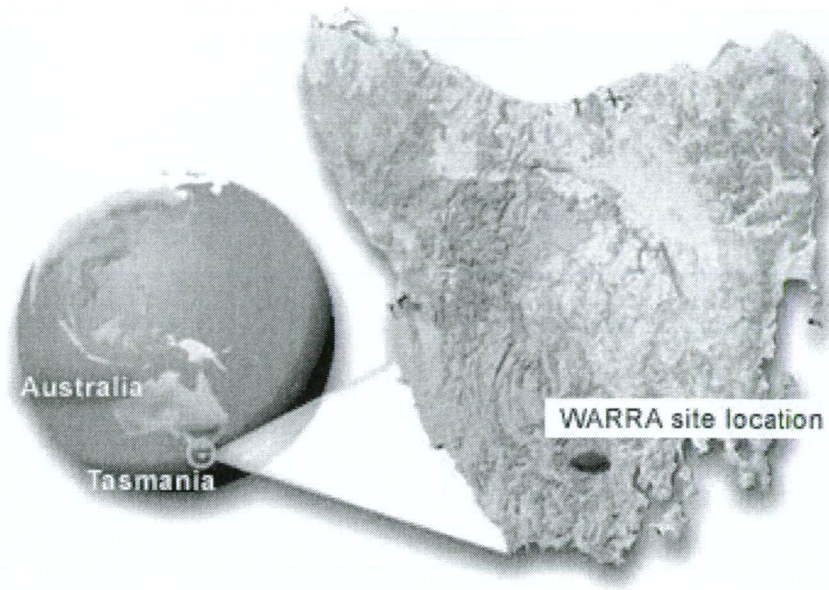
Figure 2.1 Location of the study area in southern Tasmania, Australia
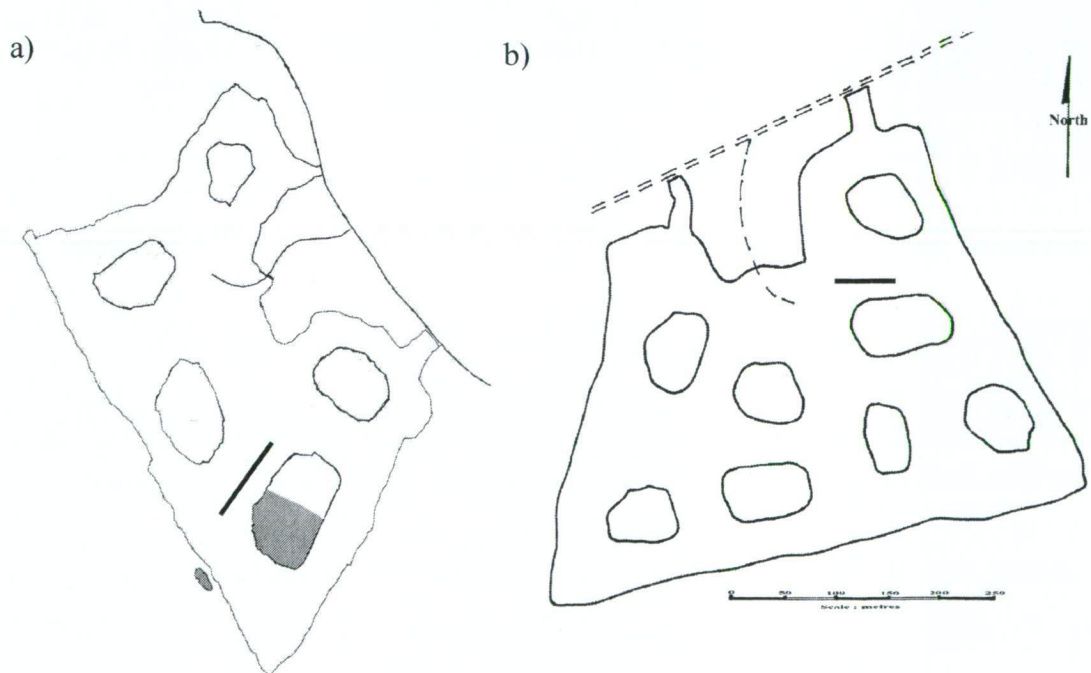
Figure 2.2 Location of 100 m by 10 m transects (━━) for Study One in Aggregated Retention Coupes (a) WR008I (grid reference 473785E, 5228171N) and (b) WR001E (grid reference 474935E, 5228057N) and area from which trees were selected (▆) for Study Two from within coupe and from streamside reserve of (a) WR0081. Maps provided by Forestry Tasmania.

The Warra LTER site is located approximately 60 km south-west of Hobart (43° 04'S, 146° 41' E) and was established in 1995 to investigate the biodiversity and ecological processes within wet *E. obliqua* forests (Brown *et al.* 2001). A particular focus is the assessment of the ecological, social and economic impacts of a range of silvicultural alternatives to CBS silviculture (Hickey *et al.* 2001).

The forest was multi-aged wet eucalypt forest dominated by *Eucalyptus obliqua*, some of which had been selectively and salvage logged prior to the 1960's (Alcorn *et al.* 2001). Two 'aggregated retention' coupes WR008I and WR001E that were located less than 1km apart and undergoing logging as part of a silvicultural trial were used for Study One, and one of these coupes was used for Study Two (WR008I). Both coupes had similar understorey species composition, slope and aspect, and are described in detail in Alcorn *et al.* (2001).

Three age-classes (> 150, 105 and 69 years old) were present on each coupe. The two youngest age-classes resulted from major wildfires in 1898, and 1934 (Alcorn *et al.* 2001). These age-classes (69 and 105 years old) were confirmed by ring counting. The oldest age-class contained trees that had survived both fires events; however the exact age of individual trees was undeterminable. This area was chosen for Study One as it was possible to access the trees as they were felled, and as the site had trees of ages just under the current prescribed rotation length (69 year old), just past the current prescribed rotation length (105 years old) and commercially over-mature (> 150 years old). Throughout this thesis the tree age-classes are referred to as *young* (69 years old), *medium-aged* (105 years old) and *old* (>150 years old).

This site was also considered to be suitable for Study Two as the partially logged coupe partly imitated the more open forest conditions that would be expected after a wildfire.

2.3 STUDY TREES

Study One- Saproxylic beetles inhabiting living E. obliqua and their habitat associations

Six *E. obliqua* trees in each age-class (4 trees in each age-class from WR008I and 2 trees in each age-class from WR001E) were selected along a 100 m by 10 m

transect within each coupe (Figure 2.2). The first 2 or 4 trees along each respective transect within each age-class were selected, provided they fitted specific selection criteria. These criteria were as follows:

1) Trees must be within a similar size-class for each age-class (based on diameter at breast height over bark (DBHOB));

2) Trees must be able to be safely felled and removed;

3) Variables such as aspect and slope should be kept as constant as possible.

Attributes of each tree were detailed prior to felling; this included DBHOB and the location of each tree in relation to each of the others.

Table 2.1. Selected architectural features of all eighteen sampled trees from Study One. Tree age-class was verified by counting growth rings of each individual[*]. Standard error is shown.

Tree Code	Age-class	DBHOB (cm)	Tree Height (m)	Number of Stem Hollows	Fire Scar Area (m^2)	Number of Large Dead Branches[#]	Dead Top Present
T41	Young	24	19	0	0	0	No
T9		29	24	0	0	0	No
T25		29	27	0	0	0	No
T43		30	25	0	0	0	No
T24		31	26	0	0	0	No
T7		41	23	0	0	0	No
Mean		30.6±2.29	24±1.16	0	0	0	
T10	Medium	43	31	0	0	4	No
T30		43	28	0	0	5	No
T2		64	30	0	0	0	No
T40		64	33	0	0	0	No
T42		64	32	0	0	0	No
T3		76	32	0	0	0	No
Mean		59±5.40	31±1.78	0	0	1.5±0.96	
T6	Old	73	23	1	0.40	5	Yes
T4		95	21	0	1.81	3	Yes^
T44		96	22	0	0.47	2	Yes^
T5		99	30	1	0.26	10	Yes
T45		99	39	2	1.16	6	Yes^
T21		111	28	0	2.54	2	Yes^
Mean		95.5±5.07	27.2±2.77	0.7±0.33	1.11±0.37	4.7±1.26	

[*] *Tree age in the oldest age-class (>150) could not be verified by ring counting due to extensive stem decay. Tree age may range from 150 years to more than 350 years old.*
[#] *Large dead branches are those >5cm in diameter.*
^ *Beetles sampled from these hollows*

Trees were felled by professional logging contractors and were removed to a clearing near the landing for further analysis. The trees had to be moved for safety

considerations. The trees' condition was assessed at the clearing; if too much damage (loss of a large proportion of branches or bark) had occurred during this process trees were rejected and replaced by other trees.

Several attributes were measured for all trees: height, the dimensions (length, circumference or depth) and location (height and aspect) of all branches, knots, fire scars and hollows.

Study Two- Role of saproxylic beetles in habitat formation and their association with fire

Forty-five *E. obliqua* trees were selected from two plots (30 trees from within one retained aggregate and 15 trees from the coupe's streamside reserve) within or adjacent to the aggregated retention coupe WR008I (Figure 2.2). The first 15 or 30 trees encountered within each plot were selected, provided they fitted specific selection criteria. These criteria were as follows:

1) Trees must be from the young (69 years old) or medium-aged (105 years old) age-class;

2) Trees must not have any discernible wounds from the logging operation.

Table 2.2 Selected measured attributes of all sample trees from Study Two. Tree distance from edge was measured to the closest harvested area regardless of aspect and rounded to the nearest metre.

Burnt Trees			Wounded Trees			Control Trees		
Tree Code	DBHOB (cm)	Distance from Edge (m)	Tree Code	DBHOB (cm)	Distance from Edge (m)	Tree Code	DBHOB (cm)	Distance from Edge (m)
W01	14	4	W02	25	5	W06	63	14
W03	33	6	W04	32	8	W19	64	12
W05	36	14	W07	20	9	W21	22	0
W08	42	7	W09	58	10	W24	67	17
W12	32	1	W10	49	9	W25	46	13
W15	60	1	W11	47	2	W33	14	2
W17	62	14	W13	50	0	W34	20	4
W18	24	9	W14	25	0	W38	29	8
W22	46	2	W16	44	9	W43	33	0
W23	37	10	W20	29	6	W45	54	3
W31	27	0	W32	22	0	W50	223	0
W35	55	5	W37	21	8	W51	83	6
W36	46	0	W39	35	8	W52	111	0
W40	22	8	W41	29	0	W53	106	5
W44	18	2	W42	35	4	W54	147	18

Attributes of each tree were recorded, this included DBHOB, location of each tree within the aggregate and in relation with each other.

2.4 SAPROXYLIC BEETLE SAMPLING METHODS

Study One

Saproxylic beetles were sampled from adjoining stem sections for each tree using two methods: destructive sampling and emergence trapping (Figure 2.3). This study was conducted in conjunction with another PhD student (Anna Hopkins) studying wood-decay fungi. The same standard sampling sections were used for both studies to investigate the relationship between beetles and wood decay fungi. Additional wood fractions (hollows, knots and branches) were studied only for saproxylic beetles. The standard sections were chosen as they have been found to be concentration points for decay in other studies (Wardlaw 1996; Wardlaw 2003). This would therefore be ideal for sampling saproxylic beetles which are often associated with decomposing heartwood (Speight 1989). Sampling point 1 (at 11-12m up the stem) represented decay within the main stem of each tree and encompassed the zone, identified by Wardlaw (2003), of 6-12 m height up the main stem as one being particularly prone to stem decay. Sampling point 2, immediately below the crown, incorporated the majority of senescent branch stubs which may act as entry points for fungi (Wardlaw 1996). Finally, sampling at point 3 included large living or dying branches within the crown, which may also be useful entry points for stem decay fungi.

Sections samples for decay and fungi

Sections sampled for beetles

Within the crown

At each sampling point :

Below the crown

One ½ metre billet was destructively sampled for beetles.

The other ½ metre billet was placed in an emergence trap and emerging beetles were captured for two years.

11-12m (main stem)

The three upper cut faces were examined for decay. Samples of decayed wood were excised for isolation of associated wood decay fungi in a separate study by Anna Hopkins.

Figure 2.3 Tree sampling method used in Study One, showing three standard sampling heights, each cut into two ½ metre billets. Diagram produced in conjunction with Anna Hopkins.

Destructive Sampling

Destructive sampling is a direct method for actively searching for beetles in a substrate. It is a time consuming and laborious form of collecting, but has the advantage of providing information about the biological traits of a species. Knowledge is gained on respect to the location of the beetle in the substrate (e.g. in the solid wood or decayed wood; sapwood or heartwood); the life history, such as the presence of larvae and adults in the same areas; and the likely feeding guild.

The method used was modified from Yee (2005). Trees were felled and three half-metre wood sections cut out of the stem at standard sampling points (Figure 2.3).

Wood sections were split into small pieces using a tomahawk and mallet, with particular attention focused on signs of insect activity within the wood (such as galleries, frass or holes). Any beetles (adults or larvae) were collected using forceps. Adults were placed in 70-80 % ethanol for subsequent identification. Larvae were either stored in 70-80 % ethanol (large larvae were placed in boiling water first to prevent enzymatic breakdown), or placed alive for rearing in small containers with some of their original substrate (solid wood, rotten wood). Records were made of beetle location within the stem (sapwood, inner or outer heartwood) and type of wood (solid/rotten) from which they were collected. Rotten wood pieces were retained for classification into rotten wood types.

When wood was decayed to the extent that it was humus-like (usually in the central part of the stem) it was collected, weighed, and in the laboratory sieved under lights. All beetles including fragments of beetles were collected.

Emergence trapping

Emergence trapping is a passive method that allows the collection of quantitative samples of beetles over a period of time from a known substrate. The establishment cost of emergence trapping is quite high but the method provides important information about direct associations with a substrate. Emergence trapping allows the collection of smaller beetles that are often missed with destructive sampling.

The emergence trapping in this study was designed to investigate beetle assemblages associated with both trees of different ages and within different wood fractions of each tree. Stem sections of each tree at three standard sampling points were collected (Figure 2.3). Each section had the bark removed, and bark and stem sections were placed into separate emergence bags. Additional features were also collected. Two branches and two knots (one from below the crown and one from within the crown) were sampled from most trees. Hollows and dead tops of the stem were collected when present. All different wood types were placed into separate emergence bags.

The emergence traps used in this study were a modified version of the design used previously at Warra and described by Bashford *et al.* (2001) and Yee *et al.* (2001). The trap consisted of bags of various sizes made from fine mesh <1 mm fitted with a custom-made top and bottom collection head (Figures 2.4 and 2.5). A 10 cm

opening was left in the lower corner of the mesh bag to fit the bottom collection head.

Insect movement into the collection heads was facilitated by the placement of the trap (Figure 2.4). Lighter bags containing bark or smaller branches were suspended above the ground on a simple frame. This arrangement allowed the top collection head to be fixed to the frame and the bottom collection head to be suspended freely below the mesh bag.

Wood pieces were placed in a shadehouse to prevent the wood from desiccating.

Lighter wood fractions were placed in emergence bags and suspended from a simple frame.

Heavier wood fractions were placed in emergence bags and positioned on wood pallets to raise them off the floor.
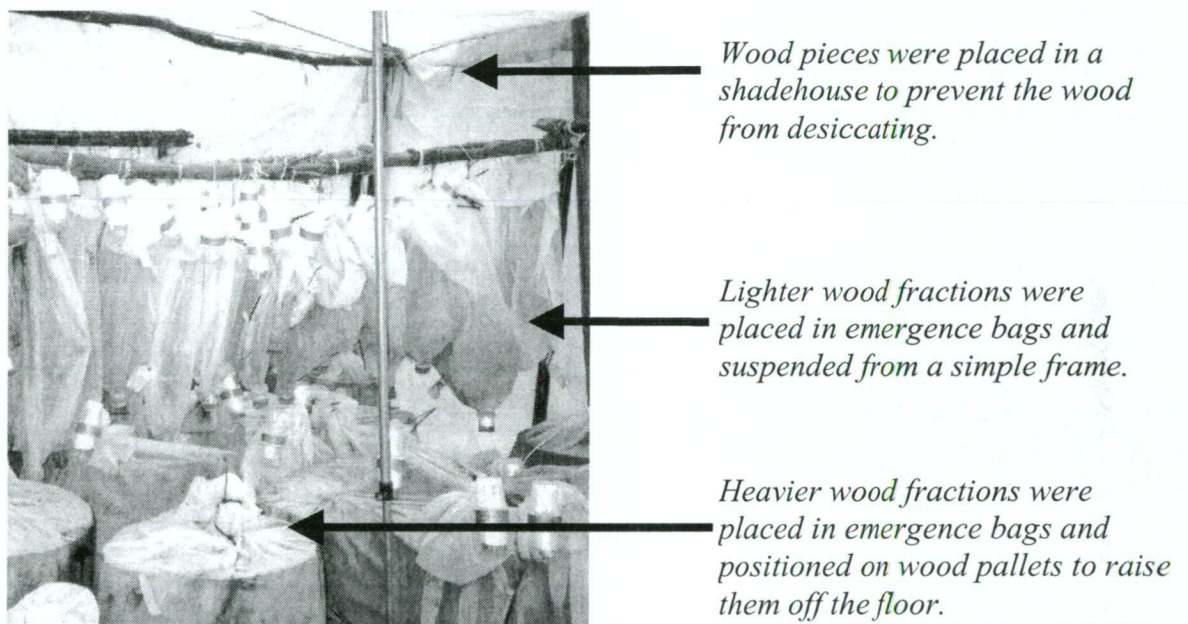
Figure 2.4 Arrangement of wood fractions (bark, branches, stems etc.) in emergence traps within the shadehouse.

Heavier traps containing stem sections, large branches, dead tops and hollows were raised above the ground with wooden boards allowing the bottom collection head to suspend above the ground and yet remain the lowest point. The top collection head was suspended above the wood section, by attachment to a large nail (Figure 2.5). All traps were placed in a purpose-built 'field' shadehouse to prevent desiccation of the wood (Figure 2.4). The shadehouse was located about 400m from the study site. Collection heads were filled with diluted ethylene glycol (50-70%) as the preserving fluid.

Top collection head which traps insects that are attracted to light. The entrance is raised above the billet to be the highest point of the trap. The jar contains diluted ethylene glycol (50-70%).

½ metre billet inside <1mm fine mesh.

Bottom collection head to trap crawling insects. This is suspended yet remains the lowest point of the trap.

Figure 2.5 Wood billet in emergence trap showing top and bottom collection heads. The emergence traps were operated for two years, after which all wood samples were destructively sampled as described above. Traps were serviced every month for the first year and every three months for the second year.

Study Two

Sample trees were randomly assigned a treatment (fifteen trees for each treatment: wound, burn, and control). Trees were wounded or burnt on their NE face at a height of 1.8 m, with a wound size of 20 cm wide x 50 cm long. Wounds were created by removing the bark and vascular cambium with a chisel and mallet to expose the sapwood. The sapwood was then further damaged by lightly scoring with a chisel (Figure 2.6). For burnt trees the exposed sapwood was additionally burnt using an LPG gas blowtorch until all the sapwood was blackened (approximately 20 minutes per tree).

Sticky trapping

Beetles attracted to the wounds were captured by sticky traps. *Sticky trapping* is a passive, principally non-substrate specific method that can be used over a period of time to collect large quantities of beetles. This type of method generally has a low establishment cost and collects a large number of invertebrates that is useful for statistical analysis.

A sticky trap (20 cm wide x 60 cm long) was constructed from wire mesh and coated with Tanglefoot®. This was nailed over half of the lower portion of the wound or burn and half over the bark beneath the wound or burn. This left the top half of the wound exposed for invertebrates to colonise (Figure 2.6).

Top half of wound was left uncovered to allow beetles to colonise. This was covered with an emergence trap after one year (see Figure 2.6).

Artificial wound (20cm wide x 60 cm long) to expose sapwood.

Lower half of wound and bark below was covered with a sticky trap consisting of 20 cm wide x 60 cm long wire mesh coated with Tanglefoot®.
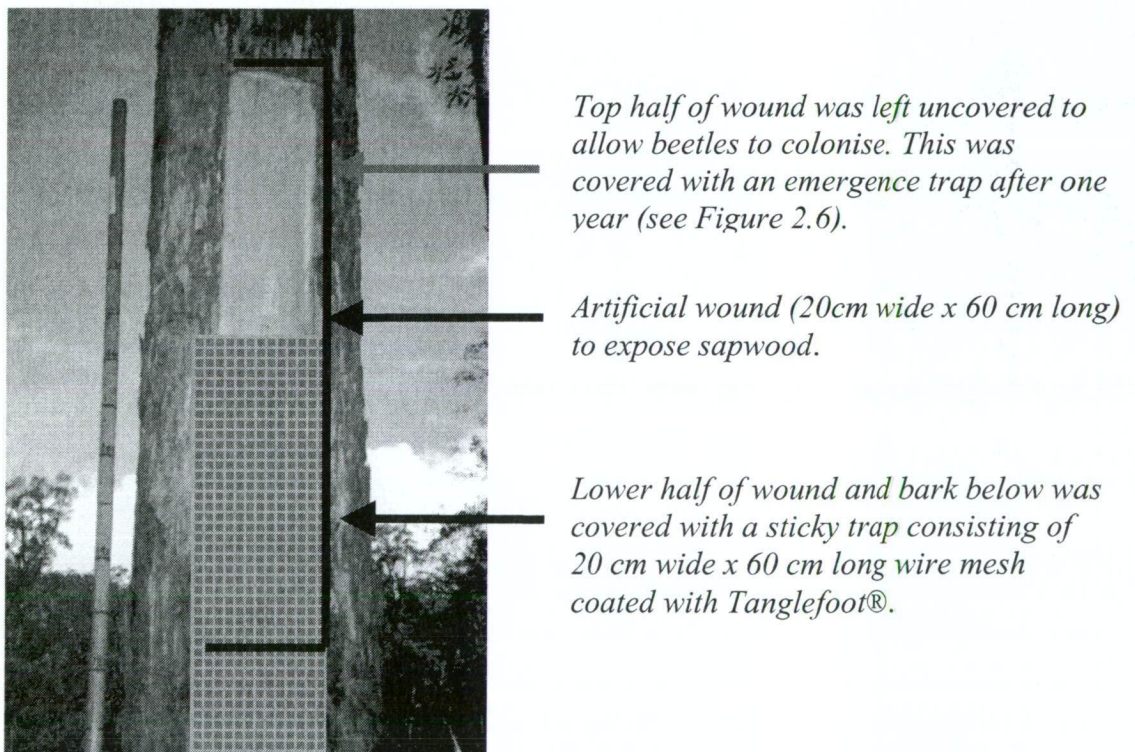
Figure 2.6 Wounded tree with an overlaid image of sticky trap indicating the location and placement of the trap over the wound.

Control trees had a sticky trap of the same dimensions attached to the undamaged stem at the same height and orientation as the damaged trees. Sticky traps were serviced every two weeks for six months, from November 2003 until April 2004.

Beetles were removed from the traps in the laboratory by handpicking using forceps under lights. They were then treated to remove the *Tanglefoot®* glue. Initially

beetles were soaked in De-Solv-it® (a citrus-based solvent) for 24-48 hours, after which the solution was then drained off. The beetles were rinsed in hot water with detergent added. Beetles were then rinsed with 80% ethanol and placed in vials containing 80% ethanol for storage.

Emergence trapping

Top collection head which traps insects that are attracted by the light.

Convex clear plastic sheet covered with <1mm fine mesh to intercept and trap beetles.

Bottom collection head to trap emerging insects which have collided with the clear plastic and fallen. The jar contains diluted ethylene glycol (50-70%).

Lower half of burn, previously covered with sticky trap.

Figure 2.7 Emergence trap covering top half of burnt treatment.

One year after the artificial damage had been created and six months after sticky trapping had ceased, the top half of all wounds and burns (which had been left uncovered to allow beetles to colonise) were covered with an emergence trap fitted with a top and bottom collection head (Figure 2.7). Control trees had an emergence trap fitted at the same height and orientation as wounded and burnt trees. Beetle emergence was monitored for six months, from November 2004 until April 2005.

Saproxylic Beetle Identification

All adult beetles were mounted and sorted into families, then into morphospecies (Oliver and Beattie, 1996). If possible morphospecies were sorted into genus and

species by comparison with the Tasmanian Forest Insect Collection (TFIC: Forestry Tasmania, Hobart), by sending specimens to the Australian National Insect Collection (ANIC, CSIRO Entomology, Canberra), by the use of taxonomic keys or by consulting with various experts. All voucher specimens have been lodged at the TFIC.

2.5 STATISTICAL ANALYSIS

The specific details of statistical methods used are discussed in each chapter, however a general outline is given below.

Univariate analyses

One-way analyses of variance (ANOVA) were undertaken in SAS 9.1 (Anon. 2002), and unless otherwise stated, a follow up multiple comparison test (Ryan-Einot-Gabriel-Welsch Multiple Range Test: REGW test) was used to determine the differences between pairs of treatment means.

Multivariate analyses

Beetles species composition for various treatments was initially compared using Non-metric Multidimensional Scaling (NMS) and Multi-Response Permutation Procedures (MRPP). Both these techniques are non-parametric multivariate statistical methods. NMS is an ordination technique that compares relative assemblage similarities in multivariate space, and MRPP uses a permutation procedure to test the hypothesis of no difference among two or more *a priori* groups based on multi-variate data. A p-value is used to evaluate whether the observed difference could be due to chance alone. Both of these were conducted using the software package *PC-ORD* version 4 (McCune and Mefford 1999). Data for NMS were $\log_{10}(x + 1)$ transformed, to reduce the dominance of the more abundant species, and calculated using a Sorenson (Bray-Curtis) distance measure, choosing the 'slow and thorough autopilot' mode. Vectors defined by beetle abundance with $r^2 > 0.2$ were overlaid. Untransformed data were used for MRPP analysis and calculated using the recommended Euclidean distance measure.

If no difference in assemblage composition for various treatments was found using unconstrained NMS ordination, then the data were also investigated using a constrained ordination technique, canonical analysis of principal coordinates (CAP), developed by Anderson and Willis (2003). This constrained ordination technique explores differences between *a priori* groups. CAP procedures were performed using a program by Anderson (2004) choosing the options of $\log_{10}(x + 1)$ transformation, the Bray-Curtis distance measure and a test of significance using 9999 unrestricted random permutations of the data. The resulting canonical axes were plotted against each other using Microsoft Excel (Microsoft Corporation 1997).

Specialists of a treatment

Species preference for various treatments was investigated using two methods, Indicator Species Analysis (Dufrêne and Legendre 1997) and correlation analysis based on canonical axes derived from CAP (as detailed by Anderson and Willis (2003)). Indicator Species Analysis was conducted using *PC-ORD* (McCune and Mefford 1999) on untransformed species data. This analysis uses the information on the concentration of species abundance to a particular group (age-class) and faithfulness of occurrence (McCune and Mefford 1999). Significance was measured using Monte Carlo randomisation procedures with IndVal $\geq$ 25, $p < 0.05$. Significant correlation was defined by $|\,r\,| > 0.3$ for each of the canonical axes obtained from the CAP output.

Mantel tests were performed in PC-ORD to compare assemblage distribution patterns such as the relationship between beetle and fungal assemblage structure in living trees. Mantel tests were based on distance matrices that had been calculated for Non-metric Multi-dimensional Scaling (NMS) in PC-ORD for each group. The Mantel tests gave p values based on randomisation (Monte Carlo) tests using 1000 randomised runs.

Chapter 3

Inventory and biology of saproxylic beetles associated with *Eucalyptus obliqua* trees

3.1 INTRODUCTION

Saproxylic invertebrates are a crucial component of the biodiversity of Tasmania's wet sclerophyll forests. Saproxylic invertebrates are a speciose group essential to the integrity of many forest processes such as decomposition and nutrient recycling. Little is known about the saproxylic fauna of Tasmania's wet forest, particularly that inhabiting older trees, and the potential impacts of forestry practices. In Northern Europe, forestry practices have played a major role in the long-term decline of many species. Baseline data provide the first step in understanding this fauna and its habitat requirements.

Previous research into invertebrates associated with living eucalypts has primarily focused on canopy or ground dwelling invertebrates (Majer *et al.* 1997). A small number of commercially focused studies have investigated wood-inhabiting or wood-feeding invertebrates as pest or potential pest species (Abbott *et al.* 1991; Elliot *et al.* 1998; Elliott and de Little 1984). Recently saproxylic species associated with *Eucalyptus obliqua* logs in southern Tasmania have been studied (Grove and Bashford 2003; Yee 2005), but to-date little is known about saproxylic species associated with the living eucalypt tree.

In parts of Northern Europe a long history of habitat alteration through human induced disturbance has resulted in many saproxylic species been considered threatened (Sverdrup-Thygeson and Ims 2002). The saproxylic fauna in Sweden is one the most comprehensively studied and over 500 saproxylic invertebrate species are red-listed (Jonsell *et al.* 1998). Many studies on the biology and ecology of these invertebrates have been conducted to find ways to reduce the threat from modern forest practices (Berg *et al.* 1994; Berg *et al.* 1995; Jonsell *et al.* 1998; Økland 1994; Ranius and Jansson 2000; Wikars 2002).

A species' vulnerability to habitat disturbance has been linked with its life history traits both theoretically and through empirical evidence. Predators and parasitoids

are generally considered more susceptible to disturbance than species directly associated with wood (Didham *et al.* 1996; Jonsson *et al.* 2005; Komonen *et al.* 2000). Other biological traits that suggest a species may be more vulnerable are poor dispersal ability (Davies *et al.* 2000; Driscoll and Weir 2005); a naturally low abundance (Davies *et al.* 2004; Davies *et al.* 2000); habitat specificity; low fecundity; narrow geographical range; and a large body size (Davies *et al.* 2000). The combination of these traits can further increase the vulnerability of a species (Henle *et al.* 2004). A species with natural rarity and a habitat specialisation could be considered at greater risk to habitat disturbance than an abundant generalist (Davies *et al.* 2004). Closely related species have been shown to sometimes behave differently in response to disturbance (Davies *et al.* 2000). This highlights the need to understand organisms at the species level wherever possible.

Understanding the ecological requirements of a species can be a step towards reducing the impact of habitat disturbance due to forestry practices. Biological surveys and published checklists are necessary to provide accessible baseline species data. The level of ecological knowledge of saproxylic invertebrate species for most of Australia is poor, limiting the potential effectiveness of forest management decisions. In the United Kingdom (Alexander 2002) and Fennoscandina (Gärdenfors 2000) the ecology, rarity and degree of threat of many saproxylic species has been collated, published and is readily available. This information cannot only be used for management decisions but can also reveal crucial gaps in the ecological knowledge of certain species. Published baseline data on a species can greatly increase the effectiveness of further studies. For example, Michaels and Bornemissza (1999) and Michaels and McQuillan (1995) found marked differences in the seasonality of activity for some species of carabid beetles. This knowledge allows further studies into these species to be designed accordingly.

This chapter documents and describes the biology of saproxylic beetles inhabiting living *Eucalyptus obliqua* trees in the wet forests of southern Tasmania by presenting results from the trapping of saproxylic beetles. Three different trapping methods were used to collect beetles. Important biological data are included and discussed. Trapping techniques are described and the advantages and disadvantages considered. The saproxylic beetle fauna in living *E. obliqua* trees in Tasmania's

southern forests is compared to the saproxylic beetle fauna from recently felled logs (Grove and Bashford 2003) and logs in an intermediate stage of decay (Yee 2005).

3.2 METHODS

Data Collection

Beetles were collected from two sites in wet eucalypt forest in southern Tasmania. Both sites were multi-aged forest with three main tree-age cohorts; two of these cohorts resulted from wildfire events in 1898 and 1934 (Alcorn *et al.* 2001; Hickey *et al.* 1998). Three different collection methods: emergence trapping, destructive sampling and sticky trapping, were used to sample saproxylic beetles from *E obliqua* trees. Detailed descriptions of these sites and methods can be found in Chapter 2.

In summary, *emergence trapping* and *destructive sampling* were conducted on three adjacent half metre stem sections from eighteen trees; six trees from three different age-classes (69, 105 and >150 years old). Additional emergence trapping was conducted on tree features such as branches, hollows and knots. The stem sections were also sampled destructive after emergence trapping ceased. Sticky trapping was conducted on 45 standing trees at one site only.

The destructive sampling method used was a variation on that used by Yee (2005). Three standard wood sections were split into small pieces using a tomahawk and mallet. If present, decayed humus-like material, generally in the centre of the stem was sieved under lights and beetles or beetle fragments were collected. For a full description see Chapter 2.

Emergence trapping was a modified version of that used by Bashford *et al* (2001) and Yee *et al.* (2001) and described fully in Chapter 2. Several different substrates were sampled separately from each tree. Three standard wood sections were taken from each stem (these were adjacent to the stem sections destructively sampled). The bark was removed from the solid wood and each placed in different emergence traps. Branches and knots were sampled from all eighteen trees and when present dead tops were also sampled (see Table 2.1). Emergence trapping was conducted for 24 months with traps serviced monthly for the first year and every three months for the following year.

Beetles were collected by sticky trapping of artificially created wounds and burns from forty-five *E. obliqua* trees (fifteen trees from each treatment: wounded trees; burnt trees; and control trees). The sticky traps were serviced every fortnight, for six months from November 2003 to April 2004. The study site and sampling methods are detailed in Chapter 2.

All beetles were mounted and sorted into families, then into morphospecies (Oliver and Beattie 1996b). If possible morphospecies were sorted into genus and species as outlined in Chapter 2.

Data Analysis

Taxonomic composition and assemblage structure

Data from all three trapping methods were pooled to calculate the overall taxonomic composition collected from *E. obliqua*. Species rank distribution was tested using the computer program *Species Diversity and Richness* (Henderson and Seaby 1998). The degree to which sampling effort had effectively captured total species richness was analysed using a randomised species accumulation curve calculated using *EstimateS Version 7* (Colwell 2005).

Biological traits

Few studies have been conducted on the saproxylic beetle fauna from Tasmania's southern forests. Recent studies by Michaels and Bornemissza (1999), Yee (2005) and Grove and Bashford (2003) have increased the knowledge about the fauna present and its ecological role. Data presented on the biological traits of these beetles have been collated from a variety of sources. Personal observations of species biological traits (such as habitat associations) from destructive sampling were initially used. If this was not available, information was derived from Yee (2005) who used a combination of resources to determine the biological traits of a species. These included personal observations, information from beetle experts and any published scientific records. If no other data were available she made inferences from species of the same genera/sub-family/family. For collected

species not in common with Yee (2005), biological traits were determined using a similar variety of sources. The main consulted references were Alexander (2002), Grove *(pers. comm.)*, Harde (1984), Lawrence and Britton (1994), Lawrence (1999), Matthews (1984; 1984; 1985; 1992; 1997; 2002).

Saproxylicity

A species was defined as *obligately* or *facultatively* or *non-saproxylic* depending on its apparent reliance on dead wood. Obligate saproxylic species require dead wood or another species that is dead wood dependent to complete their lifecycle (Speight 1989). This includes predators of dead wood dependent species and species that feed on the fungi present on dead wood. Facultative species regularly utilise dead wood as part of their lifecycle but this can be interchanged with other similar substrates such as leaf-litter or soil/humus. Non-saproxylic species do not require or use dead wood as part of their lifecycle. Only saproxylic species were used in the analysis.

Habitat

A single tree offers a large array of different habitats which are utilised by many different beetle species. A total of eight broad habitats were defined: ground/bark surface; bark; subcortical layer; solid wood; rotten wood; insect burrows; wet cracks; fungi and "unknown". In the case when a beetle or larva was located through destructive sampling, the information was used to class the beetle species to a habitat type. In most cases, literature was used to provide the best approximation of the species' habitat.

- Ground/bark surface species were species whose recorded habitat is the surface layer of a tree or log and/or the decomposition layer of a log and leaf litter.

- *Bark* species were defined as living within the bark layer of a tree or log.

- *Subcortical* species are those found underneath the bark in the sapwood.

- *Solid wood, rotten wood, insect burrows and wet cracks* are self-explanatory and are located within the bole of the tree.

- *Fungi* refers to the habitat of fungal fruiting bodies. Fruiting bodies were not present on the trees at the time of felling but did develop on some of the wood pieces used for emergence trapping.

Feeding guild

Guild classifications are based on the major feeding stage, which is the period of greatest trophic interaction with the environment. In most cases this is the larval phase of the lifecycle, which generally feeds on a different substrate from the adult phase (Bickel and Tasker 2004). In total, four different feeding guilds were defined.

- *Predatory* species are those that generally feed on any living arthropods.

- *Mycophagous* species were defined as feeding on any fungal material including fungal fruiting bodies, hyphae or spores.

- *Saprophagous* species are detritivores and feed on any dead plant or animal material or microorganisms associated with detritus.

- *Xylophagous* species are those that feed on live or dead wood. Some of these species are able to digest cellulose with enzymes produced by symbiotic microbes present in the gut.

- *Unknown* category contains species that could not be classified into a feeding guild.

Dispersal mode

An insect may disperse as an adult either by flying or crawling. Crawling species were identified by reference to literature or by the presence of fused elytra. If the dispersal mode could not be proved conclusively as crawling the species was defined as a flyer.

Body size

Body length was used as a surrogate for body size. Body length was measured using a stereomicroscope to the nearest 0.1mm. The average body length was calculated on up to four individuals per species.

Emergence time

The number of beetles captured from all emergence traps was pooled for each trapping period. The emergence time data were kept separate for the first and second year of sampling, as the trapping period was monthly for the first year of sampling and then every three months for the second.

Comparison of the saproxylic beetle fauna of E. obliqua *living trees and logs*

The saproxylic beetle fauna captured from this study of 18 living *E. obliqua* trees is compared to that of 12 recently felled *E. obliqua* logs (Grove and Bashford 2003) and 104 *E. obliqua* logs at an intermediate decay stage (Yee 2005) in the Warra region. Saproxylic beetles were captured by two collection methods (emergence trapping and destructive sampling) for logs in an intermediate decay stage and the living tree. Only one collection method (emergence trapping) was used for the recently felled logs.

Comparison of trapping methods

The saproxylic beetle assemblage composition collected from the three trapping techniques used in the present study was compared. Destructive sampling and emergence trapping was conducted on an equal volume of adjacent stem sections, allowing direct comparison of these two techniques. The sticky trapping was conducted as part of a manipulative study, in which the trees were subjected to various wounding treatments. Whilst the beetle species collected from this study provide valuable information for a list of species associated with *E. obliqua*, the study cannot be accurately used as a comparison with the other two trapping

methods. Chi-squared tests were used to test for difference in individual abundance of the most frequently occurring beetles species collected by destructive sampling and emergence trapping. Species were classified as frequently occurring if they were collected from 25 % of sampled trees.

3.3 RESULTS

Taxonomic composition and assemblage structure

In total, 11398 saproxylic beetles belonging to 357 morphospecies in 59 families were collected using three collection methods (Table 3.1). Overall, 35% of morphospecies could be identified to species, 61% to genus, 69% percent to subfamily/tribe and 100% to family (Appendix 3).

Table 3.1 Summary of saproxylic beetle families and species collected from E. obliqua *trees in southern Tasmania using a variety of collecting methods. Families are listed in taxonomic order (Total=357 species, 59 families) and those with more than 10 species are highlighted in bold.*

The most predominent families were Curculionidae with 45 morphospecies, and

Family	Number of Species	Family	Number of Species	Family	Number of Species
Carabidae	**11**	**Anobiidae**	**18**	Ciidae	5
Ptiliidae	2	Trogossitidae	2	**Melandryidae**	**10**
Leiodidae	6	Cleridae	8	Mordellidae	7
Scydmaeidae	6	Melyridae	2	Rhipiphoridae	1
Staphylinidae	**37**	Sphindidae	2	Zopheridae	9
Lucanidae	2	Brachypteridae	1	**Tenebrionidae**	**11**
Scarabaeidae	3	Nitidulidae	8	Prostomidae	2
Eucinetidae	2	Phloeostichidae	3	Oedemeridae	6
Clambidae	2	Silvanidae	4	Mycteridae	4
Scirtidae	**14**	Laemophloeidae	3	Pyrochroidae	1
Buprestidae	2	Phalacridae	4	Salpingidae	2
Byrrhidae	1	Cryptophagidae	8	Anthicidae	3
Eucnemidae	5	Erotylidae	5	Aderidae	3
Throscidae	1	Bothrideridae	1	Scraptiidae	2
Elateridae	**16**	Cerylonidae	3	Cerambycidae	6
Lycidae	3	**Coccinellidae**	**14**	Chrysomelidae	4
Cantharidae	3	Corylophidae	9	Anthribidae	4
Derodontidae	1	Latridiidae	8	Attelabidae	1
Dermestidae	7	Mycetophagidae	2	**Curculionidae**	**45**
Bostrichidae	1	Archeocrypticidae	2	Total	357

Staphylinidae with 37 morphospecies. The majority of beetles in both these families could not be identified to described species, but often were described to subfamily.

A randomised species accumulation curve (Figure 3.1) is not reaching an asymptote indicating that the sampling methods have not captured all beetle species associated with *E. obliqua* in this area.
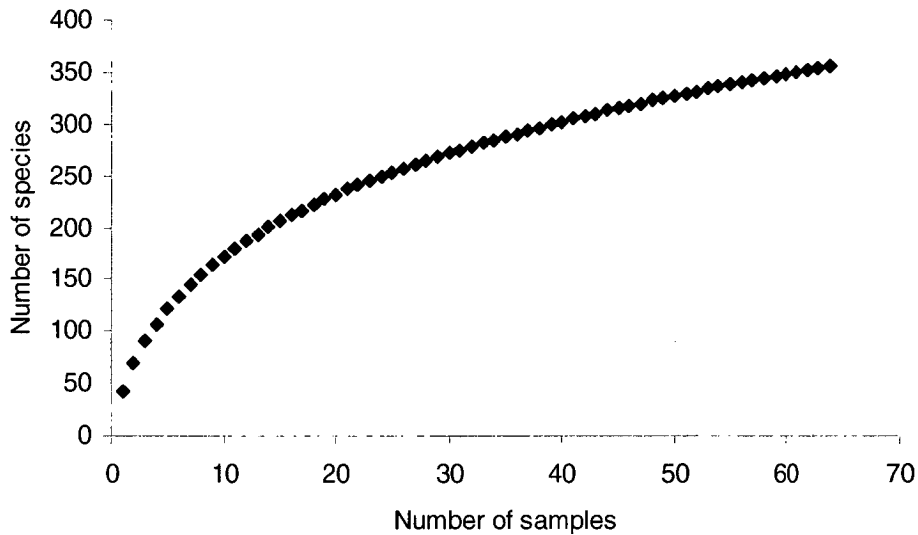
Figure 3.1 Randomised species accumulation curves for beetles collected from E. obliqua *with data from all three trapping methods pooled.*

Biological Traits

Saproxylicity

From all the species collected, 207 were classed as obligately saproxylic, 150 as facultatively saproxylic and 22 as non-saproxylic (Appendix 3). The proportion of obligate saproxylic species is probably underestimated as the classification was biased against classing a species as saproxylic because if the true nature was in doubt a species was classified as facultatively saproxylic.

Habitat

The majority of saproxylic species were either epigaeic/epixyclic generalists (111 species) or rotten wood dwellers (70 species) (Figure 3.2). The habitat associations for a large number of species (86) could not be determined. The other habitat categories shared a similar number of associated species (6-19).
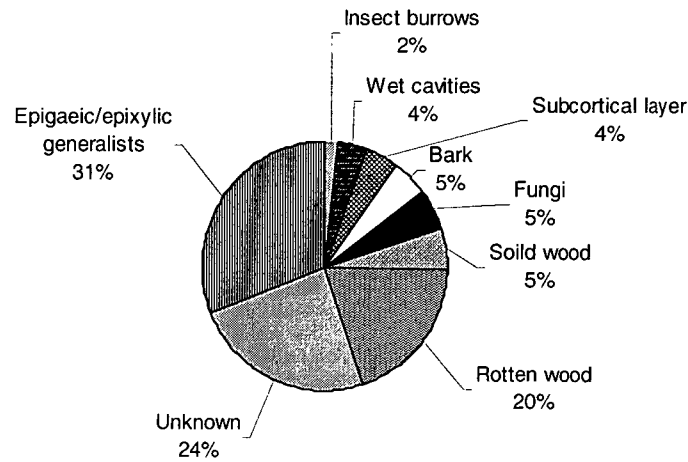
Figure 3.2 Percentage of saproxylic beetle species in each habitat type.

Feeding Guild

The three main saproxylic feeding guilds (xylophagous, mycophagous and predatory) shared a similar number of species with 92, 92 and 103 species respectively (Figure 3.3). Only three percent of the species could not be assigned to a feeding guild.
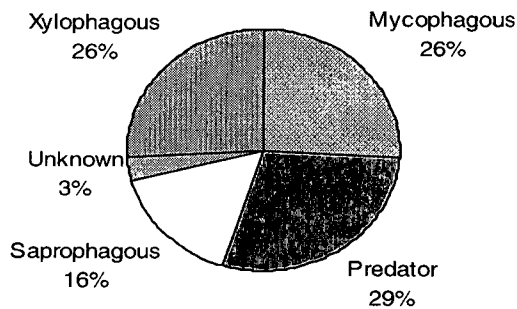
Figure 3.3 Percentage of saproxylic beetle species in each feeding guild.

Dispersal mode

The majority of saproxylic species captured were flyers (Figure 3.4). Only a small number of species were not able to be classified into a dispersal mode.
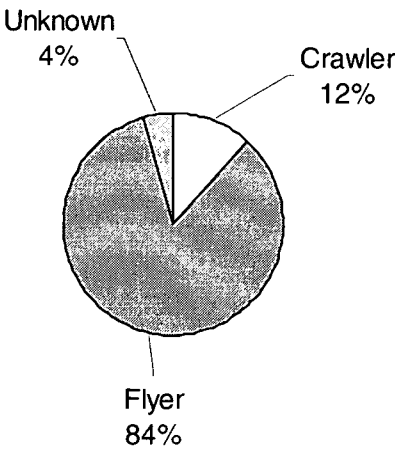
Figure 3.4 Percentage of saproxylic beetle species in each feeding guild.

Ninety percent of the species that dispersed by crawling could be attributed to two feeding guilds, predatory (45%) and xylophagous (45%) (Figure 3.5). The majority of saprophagous and mycophagous species dispersed by flying.
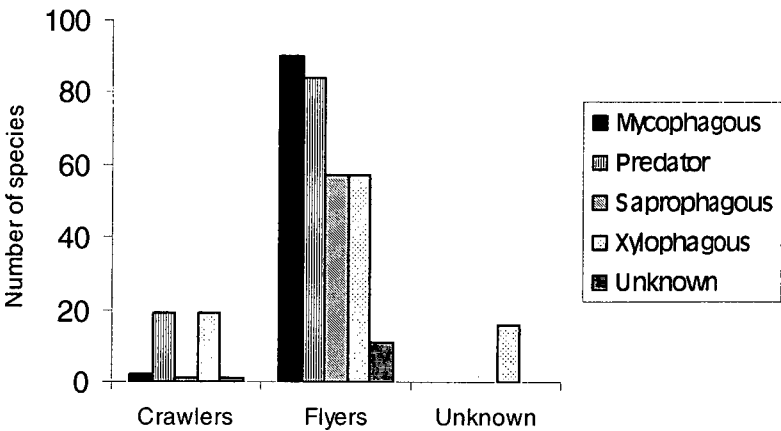
Figure 3.5 Number of saproxylic beetle species in each feeding guild and each dispersal mode.

Body Size

The body length of saproxylic beetles collected varied from 0.6 mm (*Sericoderus* TFIC sp 06, Corylophidae) to 41 mm (*Toxeutes arcuatus,* Cerambycidae). Over 69% of beetles had a body length less than 4 mm (Figure 3.6).
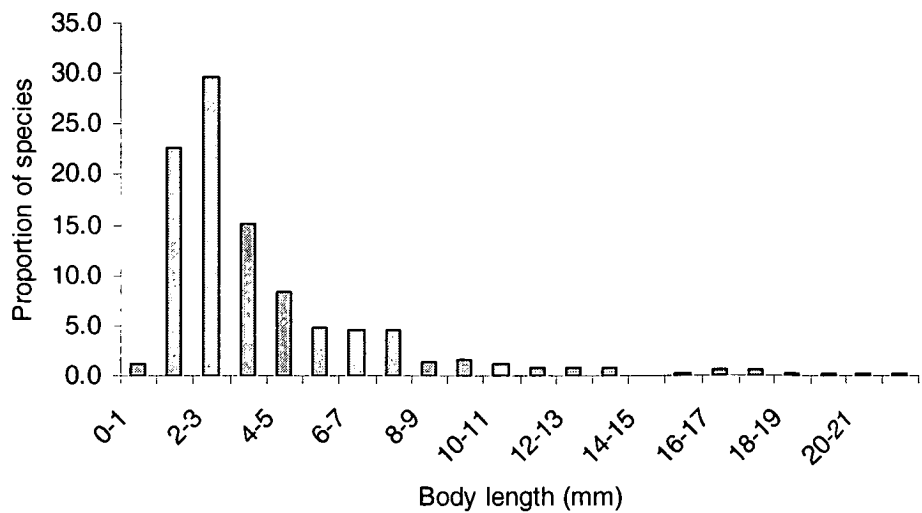
Figure 3.6 Proportion of saproxylic species for each body length range.

The range of body lengths varied considerably with each feeding guild.
Mycophagous beetles had the smallest range in body length, from 0.6 mm to
7.7 mm (Figure 3.7).
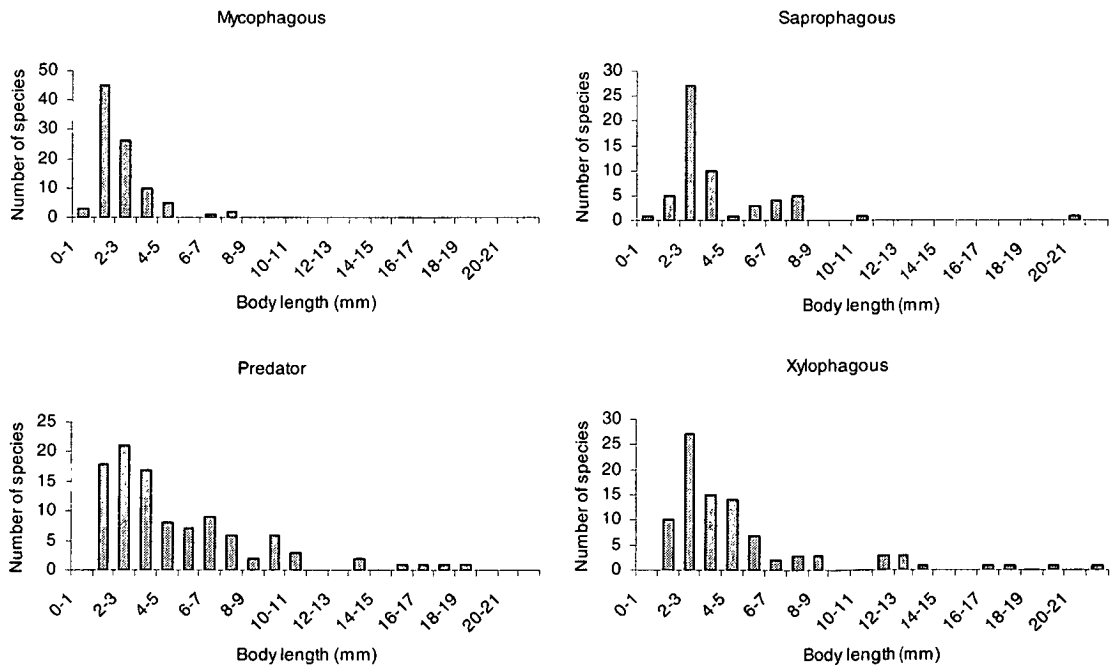
Figure 3.7 Number of species in each feeding guild for each body length range.

Ninety-one percent of all mycophagous species had a body length less than 4 mm.
Saprophagous species had a wider range of body lengths, from 0.9 mm

(Cryptocephalinae KH sp 01, Chrysomelidae) to 20.1 mm (*Meneristes australis,* Tenebrionidae). As with the mycophagous guild, a large proportion of species (74%) had a body length of less than 4 mm. Almost two-thirds of the species (64%) had a body length of 2-4 mm. Predatory and xylophagous species had a large range of body lengths (1.0 mm to 18.5 mm and 1.1 mm to 19.8 mm respectively). Almost half the species for these two guilds (predatory, 46% and xylophagous, 43%) have body lengths greater than 4 mm.

Emergence time

There was a strong seasonal effect on the time of beetle emergence, with the largest number of beetles emerging in late spring and summer, peaking in mid-summer (Figure 3.8 and 3.9). The number of beetles emerging decreased in the second year of trapping (Figure 3.9). Even at the end of two years new beetle species were still emerging (Figure 3.10). The number of beetles emerging for each trapping period is shown in Appendix 3.
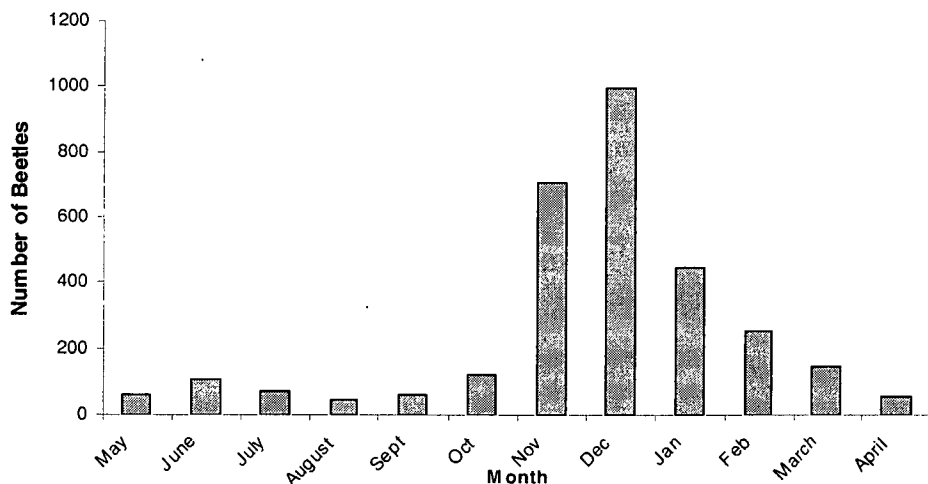
Figure 3.8 Number of beetles emerging from E. obliqua *wood sections each month in the first year of trapping.*

Four general patterns for time of beetle emergence were identified. Some beetle species such as *Aridius nodifer* (Latriididae) were collected in every trapping period, with the abundance varying seasonally. Others species tended to emerge seasonally; each late spring and summer (*Scraptia laticollis,* Scraptiidae); in the first spring/summer season only (Laemophloeidae TFIC sp 03, Laemophloeidae); or in the second spring/summer season only (*Sericoderus* TFIC sp 03, Corylophidae).
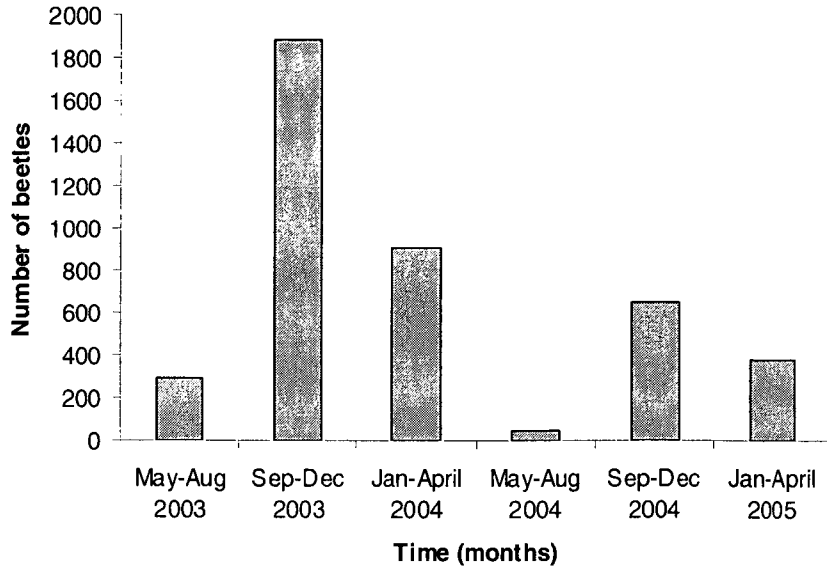
Figure 3.9 Number of beetles emerging from E. obliqua *wood sections in each trapping period.*
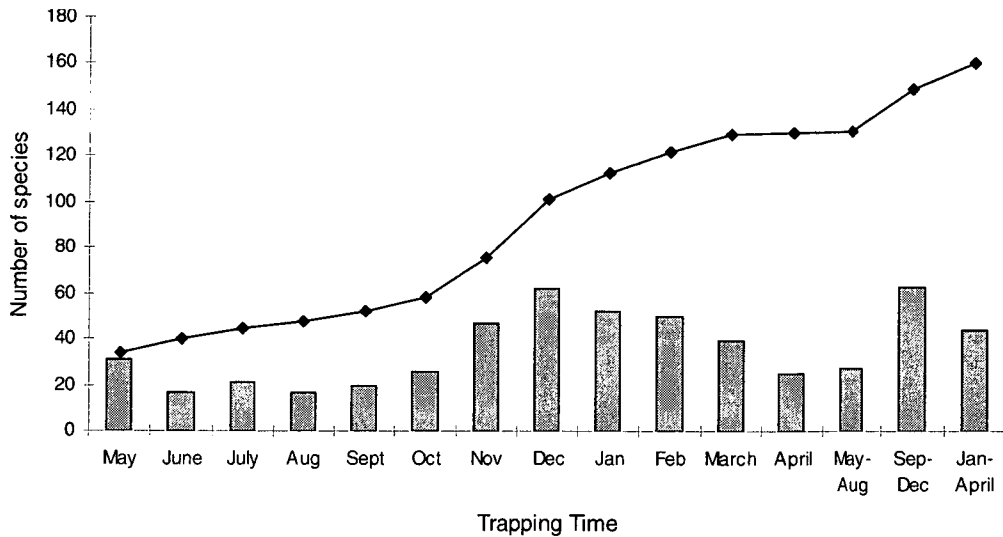
Figure 3.10 Total number (bars) and cumulative number (line) of beetle species emerging from E. obliqua *wood sections over two years of continuous sampling. Note: Time period changes during graph*

Comparison of saproxylic beetle fauna of E. obliqua trees and logs

Logs (saproxylic beetle data combined from recently felled logs and logs in an intermediate decay stage) were found to support more unique beetle species than did trees (Figure 3.11). However, both logs and trees supported many species only collected from each respective substrate. A quarter of beetle species were found in both trees and logs, indicating that either substrate may be suitable for these species.
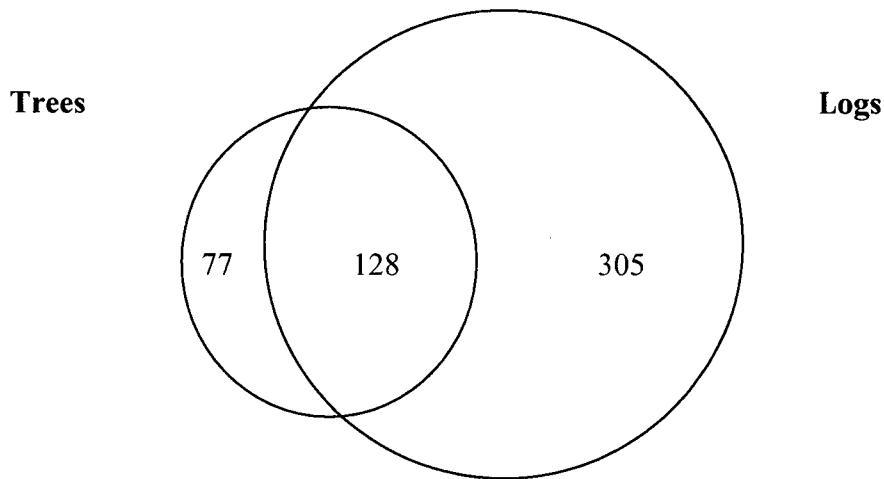
Figure 3.11 Venn diagram showing distribution of saproxylic beetle species in
E. obliqua *trees (from this study) and logs (from Yee (2005) and Grove (2003)).*
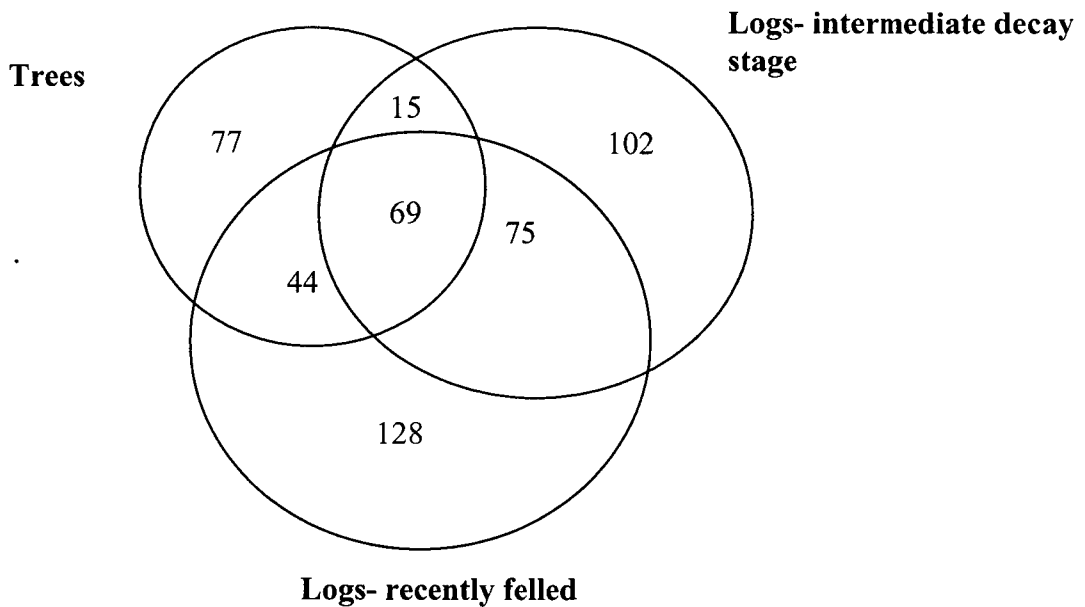
Figure 3.12 Venn diagram showing distribution of saproxylic beetle species in
E. obliqua *trees (from this study), recently felled logs (from Grove (2003)) and logs*
in an intermediate decay stage (from Yee (2005)).

A greater number of beetle species are common to newly felled logs and logs in an

intermediate decay stage, than to trees and either log substrate (i.e. recently felled

logs and logs in an intermediate decay stage) (Figure 3.12).

Comparison of trapping methods

Comparing all trapping methods

All trapping techniques captured beetles unique to that method (Figure 3.13).

Sticky trapping captured the greatest number of exclusive species (41% of all species), followed by emergence trapping (15% of all species) and destructive sampling (4%). Only ten percent of all species were collected by all three methods. Emergence trapping and sticky trapping had the largest number of species in common (35%).

Emergence Trapping **Destructive Sampling**

53   11   13

37   8

88

147
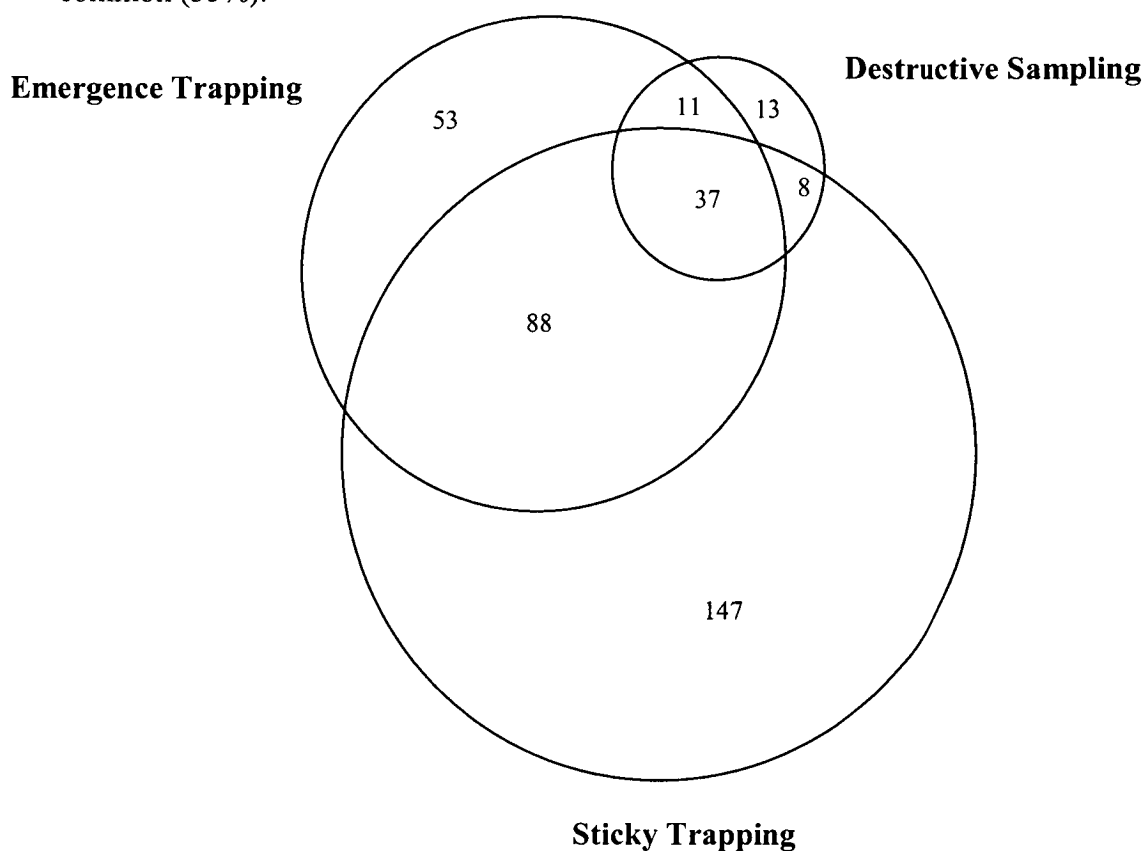
Sticky Trapping

Figure 3.13 Venn diagram showing the number and overlap of species for each trapping type.

Sticky trapping captured species in six families that were not collected by either destructive sampling or emergence trapping (Buprestidae, Ciidae, Eucinetidae, Mordellidae, Pyrochroidae and Rhipiphoridae) (Appendix 3). Emergence trapping captured species in three beetle families (Byrrhidae, Derodontidae, Lucanidae) not collected by other methods. Destructive sampling had the poorest representation of families with less than half (26 families) the total number of families captured (by this method).

Comparing destructive sampling and emergence trapping

Emergence trapping and destructive sampling were conducted on the same trees, allowing direct comparison of the two methods.

Table 3.2 Most frequent beetle species (present in a quarter of trees) captured from stem sections, showing the number of individuals captured by destructive sampling and emergence trapping. A Chi-squared test was used to calculated significant difference, indicated by * on significantly higher figure.

Family	Species binomial	DS	Emg	Total
Carabidae	*Trechimorphus diemenensis*	9	54*	63
Ptiliidae	Ptiliidae TFIC sp 01	1	40*	41
Leiodidae	*Nargomorphus* TFIC sp 02	0	16*	16
Staphylinidae	Aleocharinae TFIC sp 07	0	9*	9
	Aleocharinae TFIC sp 10	0	8*	8
	Aleocharinae TFIC sp 13	0	65*	65
	Aleocharinae TFIC sp 14	0	5*	5
	Anabaxis CHANDLER 'Type 1'	2	3	5
	Euplectops CHANDLER 'Tasmania 1'	0	17*	17
	Falagria TFIC sp 01	1	145*	146
Lucanidae	*Syndesus cornutus*	21*	9	30
Clambidae	*Clambus bornemisszai*	0	15*	15
	Sphaerothorax tasmani	1	8*	9
Scirtidae	*Prionocyphon?* TFIC sp 01	1	6	7
Elateridae	*Augenotus quadriguttatus*	1	6	7
Nitidulidae	*Brachypeplus planus*	3	35*	38
	Epuraea victoriensis	1	289*	290
Phloeostichidae	*Hymaea succinifera*	0	15*	15
Cryptophagidae	*Cryptophagidae* KH sp 01	0	24*	24
	Cryptophagus gibbipennis	0	5*	5
	Cryptophagus tasmanicus	1	16*	17
Throscidae	*Aulonothroscus elongatus*	0	12*	12
Cerylonidae	*Philothermus tasmanicus*	4	7	11
Corylophidae	*Sericoderus* TFIC sp 05	0	80*	80
	Sericoderus TFIC sp 06	0	7*	7
Latridiidae	*Aridius costatus*	0	16*	16
	Aridius nodifer	0	910*	910
	Bicava verrucifera	0	7*	7
	Cortinicara REIKE sp nov 1	0	12*	12
Zopheridae	*Pycnomerus* TFIC sp 02	106*	32	138
Prostomidae	*Dryocora cephalotes*	128*	2	130
	Prostomis atkinsoni	62*	8	70
Curculionidae	*Cossonus* KH sp 01	24	17	41
	Cossonus simsoni	8	3	11
	Pentarthrum TFIC sp 03	47	39	86
	Tyrtaeosus ustulatus	12	11	23

Thirty-six species of beetles occurred in over a quarter (5/18) of the trees sampled by emergence trapping and destructive sampling (Table 3.2). Both emergence trapping and destructive sampling techniques showed a clear bias for species collected, with the total number of captures not significantly different for trapping technique for only eight beetle species. Only four species were favoured by destructive sampling. Emergence trapping collected significantly more of twenty-

four individual beetle species, with seventeen of those species only captured by this technique.

3.4 DISCUSSION

Taxonomic composition and assemblage structure

This is the first intensive study of saproxylic beetles associated with standing *E. obliqua* trees and has found standing *E. obliqua* trees to be an important habitat for saproxylic beetle biodiversity, with 357 beetle morphospecies representing fifty-nine families collected from only sixty-three trees. The true number of species associated with *E. obliqua,* even within the wet eucalypt forest of southern Tasmania, is likely to be much higher. This is indicated by both the shape of the randomised species accumulation curve for the three trapping methods, the large number of species represented by only a single individual in the species rank abundance distribution, and the localised geographic range of this study. The beetle species present in these forests have been found to vary spatially, even over the scale of a few kilometres (Yee 2005 and Baker, *in press.*). To date over 600 saproxylic beetle species have been captured from the Warra LTER site in southern Tasmania (www.warra.com.au). A large proportion of these are likely to be associated with *E. obliqua* trees or logs.

A number of the species captured in this study remain unidentified at the level of described species. Some have been matched to undescribed species in the main forest insect collection held by Forestry Tasmania in Hobart (TFIC), but eighty-five species collected by this study are not apparently held in this collection. These species are new records for this forest type and a proportion may be new to science. These species will be sent away to various coleopteran experts for further identification. This high level of undescribed species is common to studies in this region on saproxylic beetles and other cryptic taxa. Grove and Bashford (2003) were unable to identify two-thirds of the 228 beetle species collected from logs in one year from this area. A recent study on macrofungi in this region by Gates *et al.* (2005) found that less than half the 307 species collected were fully described species.

Although saproxylic beetles are known to be a speciose functional group (Grove *et al.* 2002) the number of species collected in this study associated with *E. obliqua* can be considered to be relatively high in comparison to published studies of other tree species elsewhere. In Sweden, old oaks are associated with the most diverse beetle fauna (Palm 1959). A study by Ranius and Jansson in Sweden (2000) of ninety mature or old hollow oak trees from eighteen plots captured only 120 saproxylic beetle species. In Swedish hemi-boreal forest, a seven-year study of saproxylic beetles associated with 200 stumps of four tree species collected over 47,038 individuals and 316 species (Lindhe and Lindelöw 2004). A study on *Populus* logs and snags in Canada in four sites using emergence and window traps resulted in 257 saproxylic beetle species captured (Hammond 1997). *E. obliqua* logs in wet eucalypt forests have also been shown to have a species-rich assemblage. Yee (2005) used a combination of destructive sampling and emergence trapping at eleven sites on 104 logs in an intermediate decay stage and collected 360 species from 54 families. Grove and Bashford (2003) captured 228 saproxylic species from logs in the first year of emergence trapping. Therefore, 357 morphospecies associated with 63 *E. obliqua* trees in the current study is not a suprising finding.

Biological traits

Interaction can be seen between some of the biological traits of species, such as feeding guild and dispersal ability, and feeding guild and body size. Current ecological theories pertaining to the relationship between the biological traits of a species and its habitat (Southwood 1977) and species sensitivity to fragmentation (Henle *et al.* 2004) may help explain these relationships. Yee (2005), in a study of the assemblage of saproxylic beetles in *E. obliqua* logs, found the same interaction between these biological traits and linked the results to certain ecological theories. Both this study and her study found an interaction between feeding guild and dispersal ability. The majority of species that dispersed by crawling were either predatory or xylophagous species. However, this was not the only dispersal mode, as a large number of species in these feeding guilds also dispersed by flight. This observation may be explained by Southwood's (1977) habitat theory which predicts that species with a relatively narrow habitat or feeding niche, both spatially and temporally, should have good dispersal ability. The xylophagous species that

disperse by crawling rather than flying may be those who use a habitat that is long lasting, such as solid wood or an intermediate stage of decay (Dajoz 2000) or have broader habitat requirements such as being able to utilise both solid wood and different stages of decay. This theory is supported by the observations by Ranius and Hedin (2001) who studied *Osmoderma eremita* which lives in long lasting (decades to centuries) decaying trunks of old oaks. This beetle has poor dispersal ability while the xylophagous bark beetle *Ips typographus* that requires the relatively short lasting (1-2 years) early stage of decay has good dispersal ability (Forsse and Solbreck 1985). Predators may commonly disperse by either crawling or flying, depending on their prey. Crawling species may feed on prey that is common and flightless such as snails, collembola and mites (Yee 2005). Flighted predatory species may feed on widely dispersed prey such as wood boring beetles (Lawrence and Britton 1994). Very few mycophagous and saprophagous species dispersed by crawling. The food source of species in both these guilds is fungi or detritus which is often ephemeral and patchy.

Clear trends were found between a beetle's body size and feeding guild, supporting findings by Yee (2005) and theories reviewed by Henle *et al.* (2004). The majority of mycophagous species, which are adapted to feed on minute fungal hyphae or spores, that are generally located in confined spaces such as between wood cells and lining insect galleries (Lawrence and Britton 1994), had a small body size (4 mm). Species in the xylophagous guild are also found within the wood habitat but have a much larger range in body sizes. This may be due to their ability to alter their environment and prevent it limiting their movement by feeding on the wood and hence making their habitat the size required (Yee 2005). Predatory beetles, feeding on a diverse range of organisms with varying sizes (from small collembola to larger snails), had an accordingly diverse range of body sizes.

The seasonality in abundance and activity of invertebrates is well documented, with the peak period of abundance often the late spring and summer months as in this study (Bickel and Tasker 2004; Michaels and McQuillan 1995; Wikars *et al.* 2005). The majority of beetle species from this study were successfully captured by sampling during this peak period. However, for a comprehensive biodiversity study it would be necessary for year-round sampling as some species only occurred outside of this period of peak activity. A large number of species were still

emerging from the wood after two years of sampling, with many beetle species emerging for the first time in the second year of sampling. For the beetles emerging in the second year there are two possibilities for the beetles' life history strategy; either the larval stage of the beetle is at least two years or the beetle was able to continue its natural lifecycle and continue to reproduce even with the disruption of its environment by the felling of the tree.

Comparison of saproxylic beetle fauna of E. obliqua *trees and logs*

Logs were found to support a higher number of unique species than trees. This may in part just reflect the far greater number of logs (116) sampled than the number of trees (18) sampled. Jonsell (1998) compared saproxylic species substrate associations in Sweden. Trees were found to be associated with a slightly greater number of species (317 species) than were logs (295 species). Trees were also found to have the highest proportion of species confined to this substrate type (90 species, 28% of fauna). Even with the small number of trees (18) that were sampled in this study, 77 species of saproxylic beetles were found to be only associated with trees, thus highlighting the importance of both substrate types (trees and logs) for saproxylic beetle diversity.

The two log substrates (recently felled logs and logs in an intermediate decay stage) supported a greater number of species in common than either log substrate or trees, suggesting that the habitat of living trees may be quite different from logs. Jonsell (1998) suggested that one reason for the large number of saproxylic species unique to trees was that many of the species breed in wounds on living trees, a habitat which is not present in logs. Many other factors may also influence saproxylic beetle associations with either logs or trees. These include the extent of decomposition (Dajoz 2000; Hammond *et al.* 2001; Speight 1989) and substrate orientation (Jonsell *et al.* 2004; Jonsell and Weslien 2003; Ranius and Hedin 2001).

Comparison of trapping methods

Trapping methods varied greatly in species richness, abundance and identity of collected species. Other studies have found similar results, with each trapping method having biases for different invertebrate species (Grove and Stork 1999; Hammond 1997; Økland 1996b; Ranius and Jansson 2002; Wikars *et al.* 2005; Yee

2005). All methods have advantages and disadvantages; the appropriate method to use will depend on the study being conducted and the nature of the questions asked.

Sticky trapping captured the largest number of individuals and species. However, the main limitation of this method is that there is no indication of the true nature of the species' relationship with *E. obliqua*. Some of the species, even the saproxylic species may just be 'tourists' that do not directly use the trees being sampled. The sticky trapping used in this study can be considered as a version of a flight intercept trap. Various modifications of flight intercept trapping (particularly window traps) have been commonly used to capture saproxylic beetles in Northern Europe (Hammond 1997; Jessop and Hammon 1993; Kaila 1993; Kaila *et al.* 1997; Martikainen *et al.* 1999; Økland 1996b; Ranius and Jansson 2002), Canada (Hammond 1997; Hammond *et al.* 2004) and Australia (Grove and Stork 1999). Window traps have been found to be effective for assessing stand-level differences in fauna. This is due mainly to the low cost of set-up and the large number of specimens captured allowing statistical analysis of the data (Grove and Stork 1999). Sticky trapping was used in this study as part of another research objective. Due to the lengthy processing involved, it would not be recommended for large-scale biodiversity surveys.

Both the destructive sampling and emergence trapping captured beetles that can be directly associated with the substrate. This information is particularly useful in this type of study where little is known about the saproxylic beetles and their tree species associations. Destructive sampling is very useful for providing habitat associations such as relationships with decay types investigated in other areas of this research. However, if this information is not required as a component of the study, emergence trapping alone would be recommended as an adequate method for sampling the saproxylic fauna of *E. obliqua*. The additional species captured by destructive sampling would not justify the amount of time and effort involved for a biodiversity study alone. Yee (2005) who studied the saproxylic beetles fauna of *E. obliqua* logs came to a similar conclusion. Destructive sampling is hard to standardise, with biases between collectors, as capturing a beetle depends on the collector's ability to sight them. Smaller beetles, inactive beetles, and beetles that closely resemble the substrate are often overlooked. Very active beetles often escape and different collectors tend to observe different species.

The most effective method for studying beetles directly associated with *E. obliqua* was emergence trapping. This method is substrate-specific, captured a reasonably large number of individuals, and provides biological data. The number of individuals from each species emerging per log can show assemblage structure and time of emergence (either season or year); can provide information on a beetle's life-cycle; and separating specific substrates into different emergence traps (such as bark or stem) reveals habitat associations. Additional information (such as rotten wood types present) can also be gained by investigating the wood after the trapping has ceased. Emergence trapping has been criticised in the past for providing a sample size too small for meaningful statistical analysis. For example a study by Økland (1996b) collected only 164 saproxylic beetles from 167 emergence traps on Norway spruce logs, limiting statistical analysis of the data. The current study which collected 4187 saproxylic beetles from 18 trees, and a recent study by Wikars *et al.* (2005) on Norway spruce which collected 1400 saproxylic beetles from 30 traps) did not come to this conclusion. The main disadvantage of emergence trapping is its high establishment cost.

A few commonly collected species were under-represented in the emergence trapping. All of these species were hand collected from the wood sections after cessation of the emergence trapping, suggesting the low numbers caught in emergence trapping may be due to the species having a prolonged lifecycle or low dispersal rate. Three species: *Pycnomerus* TFIC sp 02 (Zopheridae), *Dryocora cephalotes* (Prostomidae) and *Prostomis atkinsoni* (Prostomidae) were more commonly captured by destructive sampling before and after emergence trapping. Both larvae and adults were present within the same region, suggesting the beetles undergo consecutive generations without dispersing. Yee (2005) found a similar life history pattern for these species in *E. obliqua* logs. While these species were under-represented in emergence traps, some individuals were collected, and contribute to the overall species richness total. If emergence trapping had continued for a longer period of time it may have resulted in a more accurate representation of abundance for these species.

3.5 Summary

A high diversity of saproxylic beetles has been found associated with living
E. obliqua trees in Southern Tasmania's wet forests. This baseline survey (of
saproxylic species associated with *E. obliqua*) provides the first step in
understanding how to best cater for their needs in the production forest and is
explored further throughout this thesis. The accompanying species biological data
can help identify species that theory suggests may be more vulnerable to habitat
disturbance. This information makes possible more targeted studies on potentially
vulnerable species. For example, the dispersal ability of species suggested to be
poor dispersers can be established. This and other targeted studies will help
managers in planning the landscape to decrease the risk of extinction for saproxylic
species.

Emergence trapping was found to be the most effective trapping technique for
assessing beetles associated with a particular substrate. Beetle species emergence
was seasonally dependent, with new species still emerging after two years of
trapping. Therefore, for complete inventories beetle emergence trapping needs to be
continuous and over a long time frame.

APPENDIX 3.1

List of all saproxylic beetles with their biological traits, collected from living E. obliqua *trees in southern Tasmania's wet forest using three trapping methods. Abbreviations are: DS =Destructive sampling, EMG =Emergence trapping, ST =Sticky trapping, Obl = Obligate saproxylic, Fac = Faculative saproxylic, Pred = Predator, Myco =Mycophagous, Xylo =Xylophagous, Sapro =Saprophagous, Unk =Unknown, G/B Sur. = Ground/Bark Surface, Rotten =Rotten wood, Subcortical =Subcortical layer, Wet Cav =Wet cavities, Burrows =Insect burrows. The emergence times for beetles collected emerging from wood billets (Study One) are listed in month order from May 2003 – April 2004, shown by the initial of each month. Then collections were made every three months: May-August 2004 (M-A), September - December 2004 (S-D) and January - April 2005 (J-A).*

Family-Species Binomial	DS	EMG	ST	Saproxylicity	Feeding Guild	Habitat	Dispersal Mode	Body Length	M	J	J	A	S	O	N	D	J	F	M	A	MA	S-D	J-A
Carabidae																							
Adelotopus dubius dubius	1	0	10	Obl	Pred	Bark	Fly	6.9															
Agonocheila curtula	0	1	2	Fac	Pred	Bark	Fly	3.8															
Amblystomus nigrinus	0	2	0	Fac	Pred	G/B Sur.	Fly	2.4	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Carabidae KH sp 01	0	1	0	Fac	Pred	G/B Sur.	Fly	3.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Carabidae KH sp 02	0	1	0	Fac	Pred	G/B Sur.	Fly	5.8	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Dystrichothorax tasmaniensis	0	0	7	Obl	Pred	G/B Sur.	Fly	3.9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mecyclothorax ambiguus	1	8	0	Fac	Pred	G/B Sur.	Fly	4.9															
Notonomus politulus	1	0	0	Fac	Pred	G/B Sur.	Crawl	15	-	-	2	3	1	2	-	-	-	-	-	-	-	-	-
Sarothrocrepis gravis	0	1	0	Fac	Pred	G/B Sur.	Fly	4.4															
Sloaneana tasmaniae	0	1	0	Fac	Pred	G/B Sur.	Fly	4.5	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Trechimorphus diemenensis	10	90	2	Fac	Pred	G/B Sur.	Fly	4.9	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Ptiliidae									3	-	1	1	1	2	1	2	6	3	6	1	1	-	62
Ptiliidae TFIC sp 01	1	392	3	Fac	Myco	G/B Sur.	Fly	0.7															
Ptiliidae TFIC sp 04	0	27	1	Fac	Myco	G/B Sur.	Fly	1	3	6	3	5	1	3	28	132	57	22	14	6	1	5	106

Family-Species Binomial	DS	EMG	ST	Sapro-xylicity	Feeding Guild	Habitat	Dispersal Mode	Body Length	M	J	J	A	S	O	N	D	J	F	M	A	MA	S-D	J-A
Leiodidae																							
Leiodidae KH sp 01	0	2	0	Fac	Myco	G/B Sur.	Fly	2.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Leiodidae KH sp 02	0	0	1	Fac	Myco	G/B Sur.	Fly	2.8														
Myrmicholeva acutifrons	1	3	0	Fac	Myco	G/B Sur.	Fly	2.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3
Nargiotes gordoni	0	3	13	Fac	Myco	G/B Sur.	Fly	3	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1
Nargomorphus TFIC sp 02	0	67	37	Fac	Myco	G/B Sur.	Fly	2.5	1	3	4	1	2	1	11	8	10	3	7	6	-	3	7
Scydmaeidae																							
Scydmaeidae TFIC sp 01	0	1	1	Fac	Pred	Rotten	Crawl	2	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Scydmaeidae TFIC sp 04	0	3	1	Fac	Pred	Rotten	Crawl	1.3	-	-	-	-	-	-	2	-	-	-	-	-	-	1	-
Scydmaeidae TFIC sp 06	0	2	0	Fac	Pred	G/B Sur.	Crawl	1.3	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-
Scydmaeidae TFIC sp 07	0	1	0	Fac	Pred	G/B Sur.	Crawl	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Scydmaeidae TFIC sp 10	2	4	0	Fac	Pred	Rotten	Crawl	1.2	-	-	-	-	-	-	-	-	-	-	1	-	-	3	-
Scydmaeidae TFIC sp 11	0	1	0	Fac	Pred	G/B Sur.	Crawl	1.5														
Staphylinidae																							
Aleocharinae TFIC sp 02	0	10	5	Fac	Pred	G/B Sur.	Fly	3.9	-	-	-	-	-	2	3	1	1	1	2	-	-	-	-
Aleocharinae TFIC sp 03	0	2	4	Fac	Pred	G/B Sur.	Fly	2.4	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-
Aleocharinae TFIC sp 07	0	18	0	Fac	Pred	G/B Sur.	Fly	1.7	-	-	-	-	-	-	-	5	2	4	1	-	-	5	1
Aleocharinae TFIC sp 10	0	20	9	Fac	Pred	G/B Sur.	Fly	2.4	-	-	-	-	-	-	3	9	3	-	-	-	-	4	1
Aleocharinae TFIC sp 13	1	157	25	Fac	Pred	G/B Sur.	Fly	2.8	5	5	13	8	23	8	29	32	21	7	2	-	-	3	1
Aleocharinae TFIC sp 14	0	27	148	Fac	Pred	G/B Sur.	Fly	1.5	-	7	2	1	2	-	1	6	1	1	-	-	-	4	2
Aleocharinae TFIC sp 31	0	3	0	Fac	Pred	G/B Sur.	Fly	3.4	-	-	-	-	-	-	1	-	1	1	-	-	-	-	-
Anabaxis CHANDLER 'Type 1'	8	7	1	Fac	Pred	Solid wood	Fly	1.8	-	1	-	-	1	-	1	3	-	-	-	-	-	-	1
Anepius TFIC sp 01	0	0	2	Fac	Pred	G/B Sur.	Fly	1.7														
Baeocera TFIC sp 01	0	4	2	Fac	Myco	Fungi	Fly	1.5	-	-	1	-	-	1	-	-	-	-	-	-	1	1	-

Family-Species Binomial	DS	EMG	ST	Sapro-xylicity	Feeding Guild	Habitat	Dispersal Mode	Body Length	M	J	J	A	S	O	N	D	J	F	M	A	MA	S-D	J-A
Euplectops CHANDLER 'Tasmania 1'	0	39	0	Fac	Pred	G/B Sur.	Crawl	1.2	1	-	1	-	-	1	3	11	3	1	-	-	-	9	9
Falagria TFIC sp 01	1	341	3	Fac	Pred	G/B Sur.	Crawl	2.8	2	5	3	1	4	1	11	29	36	51	17	6	3	102	70
Falagria TFIC sp 04	0	2	0	Fac	Pred	G/B Sur.	Crawl	2.3	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-
Macrodicax TFIC sp 01	0	1	0	Obl	Pred	G/B Sur.	Crawl	6.7	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Paederinae TFIC sp 03	0	0	1	Obl	Pred	Burrows	Crawl	5															
Pselaphaulax CHANDLER 'Tasmania 1'	0	1	0	Obl	Pred	Subcortical	Crawl	2	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Pselaphinae TFIC sp 05	0	17	0	Fac	Pred	G/B Sur.	Fly	1.5	-	-	-	-	-	-	2	1	-	-	1	1	1	11	-
Quedius sidneensis	1	2	0	Obl	Pred	G/B Sur.	Fly	7.1	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-
Rybaxis CHANDLER 'Tasmania 1'	0	2	0	Fac	Pred	G/B Sur.	Crawl	1.6	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
Rybaxis parvidens	0	0	1	Fac	Pred	G/B Sur.	Crawl	2.2															
Sagola CHANDLER 'Tasmania 2'	1	0	2	Fac	Pred	G/B Sur.	Crawl	1.8															
Sagola rugicornis	0	2	1	Fac	Pred	G/B Sur.	Crawl	2.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Scaphisoma TFIC sp 01	0	0	1	Fac	Myco	Fungi	Fly	2.5															
Scapidiinae KH sp 01	0	0	1	Fac	Myco	Fungi	Fly	1.5															
Scapidiinae KH sp 02	0	0	4	Fac	Myco	Fungi	Fly	1.6															
Sepedophilus KH sp 01	0	1	23	Obl	Myco	Subcortical	Fly	2.3															
Sepedophilus TFIC sp 01	1	13	4	Obl	Myco	Subcortical	Fly	3.9	1	-	1	1	-	-	-	3	-	1	1	3	-	-	1
Staphylinidae KH sp 08	0	0	3	Fac	Pred	G/B Sur.	Fly	4.1															
Staphylinidae KH sp 09	0	4	0	Fac	Pred	G/B Sur.	Fly	2.1	-	-	-	-	-	-	-	3	-	-	-	1	-	-	-
Staphylinidae KH sp 10	0	1	0	Fac	Pred	G/B Sur.	Fly	6.1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Staphylinidae KH sp 14	0	2	3	Fac	Pred	G/B Sur.	Fly	1.8	-	-	-	-	-	-	1	-	-	-	-	1	-	-	-

Family-Species Binomial	DS	EMG	ST	Sapro-xylicity	Feeding Guild	Habitat	Dispersal Mode	Body Length	M	J	J	A	S	O	N	D	J	F	M	A	MA	S-D	J-A
Staphylinidae KH sp 17	0	0	1	Fac	Pred	G/B Sur.	Fly	1.8															
Staphylinidae KH sp 18	0	0	1	Fac	Unk	G/B Sur.	Fly	1.9															
Staphylininae TFIC sp 03	0	4	7	Obl	Pred	Burrows	Crawl	6.2	-	-	-	-	-	-	1	1	1	-	-	-	-	1	-
Staphylininae TFIC sp 05	0	5	0	Fac	Pred	G/B Sur.	Fly	3.4	-	-	-	1	-	-	-	-	-	-	2	-	1	-	1
Staphylininae TFIC sp 08	0	1	0	Fac	Unk	G/B Sur.	Fly	4.5	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Tasmanityrus newtoni	0	1	0	Obl	Pred	Subcortical	Crawl	1.8	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Lucanidae																							
Lissotes cancroides	6	0	3	Obl	Xylo	Rotten	Crawl	12.5															
Syndesus cornutus	30	11	0	Obl	Xylo	Rotten	Fly	12	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11
Scarabaeidae																							
Cryptodus tasmannianus	1	0	0	Obl	Xylo	Rotten	Fly	16.4															
Phyllochlaenia villosus	0	0	1	Obl	Xylo	Subcortical	Fly	8															
Saprus griffithi	0	2	4	Obl	Xylo	Solid wood	Fly	3.1	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-
Eucinetidae																							
Eucinetus TFIC sp 01	0	0	5	Fac	Sapro	G/B Sur.	Fly	2.6															
Eucinetus TFIC sp 03	0	0	8	Fac	Sapro	G/B Sur.	Fly	1.7															
Clambidae																							
Sphaerothorax tasmani	1	15	9	Fac	Myco	G/B Sur.	Fly	1.3	-	-	-	1	1	1	3	2	-	2	1	1	1	2	-
Clambus bornemisszai	0	34	21	Fac	Myco	G/B Sur.	Fly	1	-	1	-	-	-	-	12	14	-	1	3	-	-	3	-
Scirtidae																							
Prionocyphon? TFIC sp 01	1	23	530	Obl	Sapro	Wet Cav.	Fly	2	2	-	-	-	-	-	-	1	2	3	1	-	-	5	5
Pseudomicrocara atkinsoni?	0	1	1	Obl	Sapro	Wet Cav.	Fly	6.3	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Pseudomicrocara TFIC sp 01	1	0	2	Obl	Sapro	Wet Cav.	Fly	7.9															
Pseudomicrocara TFIC sp 02	0	11	455	Obl	Sapro	Wet Cav.	Fly	3	-	-	-	-	-	-	-	3	1	1	-	-	-	3	2

Family-Species Binomial	DS	EMG	ST	Saproxylicity	Feeding Guild	Habitat	Dispersal Mode	Body Length	Month of Capture in Emergence Trap														
									M	J	J	A	S	O	N	D	J	F	M	A	MA	S-D	J-A
Scirtidae KH sp 01	0	0	92	Obl	Sapro	Wet Cav.	Fly	5.1															
Scirtidae KH sp 02	0	0	1	Obl	Sapro	Wet Cav.	Fly	2.4															
Scirtidae KH sp 03	0	0	1	Obl	Sapro	Wet Cav.	Fly	2.5															
Scirtidae KH sp 04	0	0	3	Obl	Sapro	Wet Cav.	Fly	2.5															
Scirtidae KH sp 05	0	0	1	Obl	Sapro	Wet Cav.	Fly	2.6															
Scirtidae KH sp 06	0	0	1	Obl	Sapro	Wet Cav.	Fly	2.7															
Scirtidae TFIC sp 02	0	0	2	Obl	Sapro	Wet Cav.	Fly	2.4															
Scirtidae TFIC sp 04	0	0	19	Obl	Sapro	Wet Cav.	Fly	2.5															
Scirtidae TFIC sp 08	0	0	117	Obl	Sapro	Wet Cav.	Fly	2.1															
Scirtidae TFIC sp 13	0	0	5	Obl	Sapro	Wet Cav.	Fly	5.1															
Buprestidae																							
Cisseis oblonga	0	0	3	Obl	Xylo	Subcortical	Fly	6.4															
Melobasis prisca	0	0	1	Obl	Xylo	Subcortical	Fly	11.4															
Byrrhidae																							
Microchaetes bryophilus	0	1	0	Fac	Unk	G/B Sur.	Crawl	2.8	-	-	-	-	-	-	1	-	-	-	-	-	-	·	-
Eucnemidae																							
Agalba MUONA sp 01	0	0	15	Obl	Pred	Rotten	Fly	5.2															
Agalba rufipennis	0	1	13	Obl	Pred	Rotten	Fly	3.6	-	-	-	-	-	-	-	-	-	-	1	-	-	·	-
Dirrhaginae 'Muona' sp 04	0	0	1	Obl	Pred	Rotten	Fly	3.1															
Eucnemidae KH sp 01	0	0	2	Obl	Pred	Rotten	Fly	6.2															
Eucnemidae TFIC sp 04	0	0	2	Obl	Pred	Rotten	Fly	5.2															
Throscidae																							
Aulonothroscus elongatus	0	39	501	Obl	Unk	Bark	Fly	3.5	2	-	-	-	-	1	3	4	3	2	-	-	-	4	2

Family-Species Binomial	DS	EMG	ST	Saproxylicity	Feeding Guild	Habitat	Dispersal Mode	Body Length	Month of Capture in Emergence Trap														
									M	J	J	A	S	O	N	D	J	F	M	A	MA	S-D	J-A
Elateridae																							
Agrypninae TFIC sp 01	1	1	156	Obl	Pred	Unk	Fly	7.4															
Agrypnus TFIC sp 01	0	2	0	Obl	Pred	Rotten	Fly	8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Agrypnus TFIC sp 04	1	2	0	Obl	Pred	Unk	Fly	6.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Augenotus quadriguttatus	1	8	2	Obl	Pred	Burrows	Fly	9.5	-	-	-	-	-	-	-	-	2	-	-	1	-	5	-
Augenotus TFIC sp 02	1	0	0	Obl	Pred	Burrows	Fly	7.5															
Conoderus ?cordieri	0	0	4	Obl	Pred	Unk	Fly	9.7															
Conoderus australasiae	3	0	0	Obl	Pred	Bark	Fly	16.9															
Denticollinae TFIC sp 01	0	3	3	Obl	Pred	Rotten	Fly	17.5	-	-	-	-	1	-	-	1	-	-	-	-	-	1	-
Elateridae TFIC sp 05	2	1	4	Obl	Pred	Unk	Fly	5.1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Elateridae TFIC sp 09	0	0	1	Obl	Pred	Unk	Fly	7.1															
Enischnelater specularis	0	0	1	Obl	Pred	Bark	Fly	18.5															
Enischnelater TFIC sp 01	0	0	1	Obl	Pred	Rotten	Fly	9.5															
Parablax sp nr ossa	0	2	2	Obl	Pred	Unk	Fly	10.2	1	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Paracrepidomenus filiformis	0	0	1	Obl	Pred	Unk	Fly	8.7															
Pityobiinae TFIC sp 02	3	0	0	Fac	Pred	Unk	Fly	13.8															
Toorongus jugulatus	4	4	3	Obl	Pred	Unk	Fly	9.4															
Lycidae																							
Metriorrhynchus erythropterus?	1	1	5	Obl	Pred	Rotten	Fly	9.5	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Metriorrhynchus rhipidius	0	0	1	Obl	Pred	Rotten	Fly	13															
Metriorrhynchus TFIC sp 01	0	0	4	Obl	Pred	Rotten	Fly	10.6															
Cantharidae																							
Cantharidae TFIC sp 03	0	1	0	Obl	Pred	Unk	Fly	3.1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-

Family-Species Binomial	DS	EMG	ST	Sapro-xylicity	Feeding Guild	Habitat	Dispersal Mode	Body Length	M	J	J	A	S	O	N	D	J	F	M	A	MA	S-D	J-A
Chauliognathus lugubris	0	1	0	Obl	Pred	G/B Sur.	Fly	10.1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Heteromastix nigripes	0	14	150	Obl	Pred	G/B Sur.	Fly	3.7	3	-	-	-	-	-	-	2	-	3	-	-	-	5	1
Derodontidae																							
Nothoderodontus darlingtoni	0	2	0	Fac	Myco	G/B Sur.	Crawl	1.8	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-
Dermestidae																							
Anthrenocerus KH sp 01	0	0	1	Fac	Sapro	Unk	Fly	3.8															
Anthrenocerus TFIC sp 01	0	0	49	Fac	Sapro	Unk	Fly	2.2															
Anthrenocerus australis?	0	1	34	Fac	Sapro	Unk	Fly	2.1															
Dermestidae KH sp 01	0	0	2	Fac	Sapro	Unk	Fly	2.6															
Trogoderma KH sp 01	0	0	1	Fac	Sapro	Unk	Fly	2.8															
Trogoderma TFIC sp 01	0	0	1	Fac	Sapro	Unk	Fly	3.2															
Trogoderma varipes?	0	0	4	Fac	Sapro	Unk	Fly	2.9															
Bostrichidae																							
Lyctus brunneus	1	0	2	Obl	Xylo	Solid wood	Fly	3.9															
Anobiidae																							
Anobiidae KH sp 01	0	4	62	Obl	Xylo	Solid wood	Fly	2.2	-	-	-	-	-	-	-	-	-	1	-	-	-	-	2
Anobiidae KH sp 02	0	0	1	Obl	Xylo	Solid wood	Fly	1.9															
Anobiidae KH sp 03	0	2	0	Obl	Xylo	Solid wood	Fly	2.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Anobiidae KH sp 04	0	0	1	Obl	Xylo	Solid wood	Fly	2.7															
Anobiidae KH sp 05	0	0	1	Obl	Xylo	Solid wood	Fly	1.1															
Anobiidae TFIC sp 09	0	16	81	Obl	Xylo	Solid wood	Fly	2.4	-	-	-	-	-	-	-	-	-	6	-	-	-	3	5
Anobiidae TFIC sp 11	0	0	7	Obl	Xylo	Solid wood	Fly	1.3															
Anobiidae TFIC sp 13	0	0	2	Obl	Xylo	Solid wood	Fly	2.0															

Family-Species Binomial	DS	EMG	ST	Sapro-xylicity	Feeding Guild	Habitat	Dispersal Mode	Body Length	M	J	J	A	S	O	N	D	J	F	M	A	MA	S-D	J-A
Dryophilodes KH sp 01	0	10	154	Fac	Sapro	Unk	Fly	2.2	-	-	-	-	-	-	-	-	-	1	-	-	1	1	3
Dryophilodes TFIC sp 02	0	0	2	Obl	Sapro	Unk	Fly	1.9															
Dryophilodes TFIC sp 06	0	2	10	Fac	Sapro	Unk	Fly	2.7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Dryophilodes TFIC sp 10	0	0	3	Fac	Sapro	Unk	Fly	3.4															
Hadrobregmus australiensis	0	0	62	Obl	Xylo	Solid wood	Fly	4.5															
Lasioderma serricorne	0	3	14	Obl	Xylo	Solid wood	Fly	1.8	-	-	-	-	-	-	2	-	-	-	-	-	-	1	-
Ptinus exulans	0	17	14	Obl	Sapro	Unk	Fly	3.0	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Tasmanobium mimicum	0	1	5	Obl	Xylo	Solid wood	Fly	4.5	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Trypopitys multimaculatus	0	0	19	Obl	Xylo	Solid wood	Fly	4.6															
Trogossitidae																							
Egolia variegata	0	0	4	Obl	Pred	Subcortical	Fly	6.8															
Trogossitidae TFIC sp 01	1	3	8	Obl	Pred	Unk	Fly	2.8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3
Cleridae																							
Cleridae KH sp 01	0	0	1	Obl	Pred	Unk	Fly	4.2															
Cleridae TFIC sp 09	0	1	5	Obl	Pred	Unk	Fly	2.3	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Lemidia cicatricosa	0	0	1	Obl	Pred	Unk	Fly	3.5															
Lemidia hilaris	0	1	0	Obl	Pred	Unk	Fly	4.5	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Lemidia subaenea	0	1	1	Obl	Pred	Burrows	Fly	5.2	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Neoscrobiger patricius	0	2	5	Obl	Pred	Unk	Fly	7.1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
Parapylus bicinctus	0	0	7	Obl	Pred	Unk	Fly	5.1															
Tenerus abbreviatus	0	0	1	Obl	Pred	Unk	Fly	4.5															
Melyridae																							
Dasytes TFIC sp 01	0	0	2	Obl	Pred	Rotten	Fly	2.6															
Hypattalus? KH sp 01	0	1	19	Obl	Pred	Unk	Fly	1.8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1

Family-Species Binomial	DS	EMG	ST	Sapro-xylicity	Feeding Guild	Habitat	Dispersal Mode	Body Length	M	J	J	A	S	O	N	D	J	F	M	A	MA	S-D	J-A
Sphindidae																							
Aspidiphorus humeralis	0	9	17	Fac	Myco	G/B Sur.	Fly	1.4	-	-	-	-	-	-	-	1	-	-	1	-	-	-	7
Notosphindus slateri	0	0	1	Fac	Myco	G/B Sur.	Fly	2															
Brachypteridae																							
Notobrachypterus TFIC sp 01	0	1	24	Fac	Myco	Fungi	Fly	2.4															
Nitidulidae																							
Amlearcha elegantior	0	0	1	Fac	Sapro	Unk	Fly	2.5															
Brachypeplus planus	5	56	26	Obl	Sapro	Subcortical	Fly	4.4	2	-	-	-	-	1	5	1	2	15	20	2	3	1	4
Cryptarcha australis	0	0	4	Fac	Sapro	Unk	Fly	2.8															
Cryptarcha laevigata	0	0	12	Fac	Sapro	Bark	Fly	6															
Epuraea victoriensis	13	433	36	Obl	Sapro	Bark	Fly	2.4	10	32	7	13	3	2	14	204	126	5	-	-	1	-	16
Nitidulidae KH sp 01	0	1	7	Fac	Sapro	Bark	Fly	1.7	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Nitidulidae TFIC sp 02	0	0	1	Fac	Sapro	Bark	Fly	2.8															
Thalycrodes pulchrum	0	0	5	Fac	Myco	Fungi	Fly	2.2															
Phloeostichidae																							
Hymaea succinifera	0	29	1	Obl	Sapro	Bark	Crawl	3.5	-	-	2	3	2	-	3	5	-	3	2	3	2	2	2
Myrabolia grouvelliana	0	3	41	Obl	Sapro	Bark	Fly	2.0	-	-	-	-	-	-	-	2	-	-	-	-	-	-	1
Phloeostichidae KH sp 1	0	0	4	Fac	Sapro	Bark	Fly	3.5															
Silvanidae																							
Cryptamorpha optata	0	1	3	Obl	Sapro	G/B Sur.	Fly	3.4	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cryptamorpha TFIC sp 01	0	7	1	Obl	Sapro	G/B Sur.	Fly	2.7	-	-	-	-	-	-	2	1	-	1	2	1	-	-	-
Silvanidae KH sp 01	0	0	1	Obl	Sapro	G/B Sur.	Fly	2.4															
Uleiota australis	0	9	0	Obl	Sapro	G/B Sur.	Fly	7.4	-	-	-	-	-	-	1	-	1	-	-	-	-	1	6

Family-Species Binomial	DS	EMG	ST	Sapro-xylicity	Feeding Guild	Habitat	Dispersal Mode	Body Length	M	J	J	A	S	O	N	D	J	F	M	A	MA	S-D	J-A
Laemophloeidae																							
Laemophloeidae TFIC sp 01	0	0	1	Obl	Myco	Subcortical	Fly	1.8															
Laemophloeidae TFIC sp 03	0	14	9	Obl	Myco	Subcortical	Fly	1.4	-	-	-	-	-	-	2	3	1	1	-	-	-	-	2
Laemophloeidae TFIC sp 08	0	0	1	Obl	Myco	Subcortical	Fly	2.0															
Phalacridae																							
Litochrus ?alternans	1	36	222	Fac	Myco	Fungi	Fly	1.4	1	-	-	-	-	-	-	1	2	-	-	-	-	13	18
Phalacridae KH sp 01	0	0	4	Fac	Myco	G/B Sur.	Fly	1.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Phalacridae TFIC sp 01	2	43	671	Fac	Myco	Fungi	Fly	2.8	-	-	-	-	1	1	-	-	1	-	1	3	2	13	14
Phalacridae TFIC sp 05	0	0	25	Fac	Myco	G/B Sur.	Fly	1.8															
Cryptophagidae																							
Anchicera lewisi	0	2	42	Fac	Myco	G/B Sur.	Fly	1.7	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-
Cryptophagidae KH sp 01	0	25	6	Fac	Myco	G/B Sur.	Fly	1.4	2	2	1	-	-	4	4	1	-	8	1	-	-	-	2
Cryptophagidae KH sp 02	0	0	1	Fac	Myco	G/B Sur.	Fly	1.5															
Cryptophagidae KH sp 03	1	2	0	Fac	Myco	G/B Sur.	Fly	2.9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Cryptophagidae KH sp 04	0	0	1	Fac	Myco	G/B Sur.	Fly	2.3															
Cryptophagidae KH sp 05	0	0	4	Fac	Myco	G/B Sur.	Fly	2.0															
Cryptophagus gibbipennis	0	10	13	Fac	Myco	G/B Sur.	Fly	1.5	-	1	1	-	-	-	-	1	2	-	3	-	-	1	1
Cryptophagus tasmanicus	2	22	9	Fac	Myco	G/B Sur.	Fly	2.4	1	1	2	1	-	4	-	6	1	1	1	-	-	2	1
Erotylidae																							
Erotylidae KH sp 01	4	0	2	Obl	Myco	Fungi	Fly	4.6															
Thallis compta	0	3	1	Obl	Myco	Fungi	Fly	4.5	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Thallis femoralis	5	3	2	Obl	Myco	Fungi	Fly	4.3	-	-	-	-	-	-	-	-	-	1	1	-	1	-	-
Thallis TFIC sp 01	0	0	1	Obl	Myco	Fungi	Fly	2.8															
Thallis vinula	0	6	29	Obl	Myco	Fungi	Fly	4.5	-	-	-	-	-	2	1	-	-	-	2	-	-	-	1

Family-Species Binomial	DS	EMG	ST	Sapro-xylicity	Feeding Guild	Habitat	Dispersal Mode	Body Length	M	J	J	A	S	O	N	D	J	F	M	A	M-A	S-D	J-A
Bothrideridae																							
Teredolaemus leae	0	1	3	Obl	Myco	Burrows	Fly	3.5															
Cerylonidae																							
Cerylonidae KH sp 02	0	0	1	Obl	Myco	Rotten	Fly	1.5															
Hypodacnella tasmaniae	1	0	0	Obl	Myco	Unk	Fly	3.6															
Philothermus tasmanicus	4	12	1	Obl	Myco	Rotten	Crawl	2	1	-	-	-	-	-	-	2	2	1	-	-	-	2	3
Coccinellidae																							
Coccinellidae KH sp 01	0	1	0	Fac	Unk	Unk	Fly	2.9															
Coccinellidae KH sp 02	0	0	1	Fac	Unk	Unk	Fly	2.5															
Coccinellidae TFIC sp 09	0	0	6	Fac	Unk	Unk	Fly	1.8															
Rhyzobius TFIC sp 03	0	0	17	Fac	Myco	G/B Sur.	Fly	1.9															
Rhyzobius TFIC sp 04	0	0	2	Fac	Myco	G/B Sur.	Fly	4.1															
Rhyzobius TFIC sp 05	0	2	158	Fac	Myco	G/B Sur.	Fly	2.2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rhyzobius TFIC sp 06	0	0	11	Fac	Myco	G/B Sur.	Fly	1.7															
Rhyzobius TFIC sp 09	0	0	1	Fac	Myco	G/B Sur.	Fly	1.8															
Rhyzobius TFIC sp 11	0	0	28	Fac	Myco	G/B Sur.	Fly	1.8															
Rhyzobius TFIC sp 15	0	5	21	Fac	Myco	G/B Sur.	Fly	2.2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rhyzobius TFIC sp 16	0	1	0	Fac	Myco	G/B Sur.	Fly	2.0	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Rhyzobius TFIC sp 17	0	0	1	Fac	Myco	G/B Sur.	Fly	3															
Rhyzobius TFIC sp 18	0	0	14	Fac	Myco	G/B Sur.	Fly	2.5															
Rhyzobius TFIC sp 19	0	0	1	Fac	Myco	G/B Sur.	Fly	2.0															
Corylophidae																							
Holopsis TFIC sp 01	0	2	3	Obl	Myco	G/B Sur.	Fly	1.8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2

Family-Species Binomial	DS	EMG	ST	Sapro-xylicity	Feeding Guild	Habitat	Dispersal Mode	Body Length	M	J	J	A	S	O	N	D	J	F	M	A	M-A	S-D	J-A
Holopsis TFIC sp 04	0	2	1	Obl	Myco	G/B Sur.	Fly	1.3	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
Sericoderus KH sp 01	0	2	1	Fac	Myco	G/B Sur.	Fly	1.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Sericoderus KH sp 02	0	3	1	Fac	Myco	G/B Sur.	Fly	1.2	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-
Sericoderus TFIC sp 02	0	2	7	Fac	Myco	G/B Sur.	Fly	1.4	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1
Sericoderus TFIC sp 03	0	74	21	Fac	Myco	G/B Sur.	Fly	1.2	-	-	-	-	-	-	-	-	-	-	2	-	-	30	41
Sericoderus TFIC sp 04	0	2	6	Fac	Myco	G/B Sur.	Fly	1.3	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-
Sericoderus TFIC sp 05	0	169	11	Obl	Myco	G/B Sur.	Fly	1.3	-	3	4	-	-	1	15	22	7	3	11	3	2	18	78
Sericoderus TFIC sp 06	0	165	1	Obl	Myco	G/B Sur.	Fly	0.6	-	-	1	-	-	-	1	28	-	5	3	4	-	44	44
Latridiidae																							
Cortinicara REIKE sp nov 1	0	43	10	Obl	Myco	Subcortical	Fly	1.3	4	10	7	3	2	1	2	1	3	1	-	1	-	-	1
Aridius costatus	0	20	3	Fac	Myco	G/B Sur.	Fly	1.5	2	3	-	-	1	-	3	2	2	3	1	1	1	-	1
Aridius nodifer	0	1443	21	Fac	Myco	G/B Sur.	Fly	1.6	30	27	16	3	14	74	511	408	92	72	31	7	7	83	68
Bicava verrucifera	0	30	0	Fac	Myco	G/B Sur.	Fly	1.8	-	-	-	-	-	-	-	1	-	-	-	-	-	11	18
Enicmus REIKE sp nov 2	0	2	61	Fac	Myco	G/B Sur.	Fly	1.3	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
Enicmus TFIC sp 01	0	1	104	Fac	Myco	G/B Sur.	Fly	1.7															
Enicmus TFIC sp 01	0	1	104	Fac	Myco	G/B Sur.	Fly	1.7															
Latridiidae KH sp 01	0	1	1	Fac	Myco	G/B Sur.	Fly	2.8	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Latridiidae KH sp 03	0	0	1	Fac	Myco	G/B Sur.	Fly	0.9															
Mycetophagidae																							
Litargus intricatus	0	1	2	Obl	Pred	Unk	Fly	3.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Mycetophagidae KH sp 01	0	0	1	Obl	Pred	Unk	Fly	2.8															
Archeocrypticidae																							
Archeocrypticidae KH sp 01	1	0	0	Fac	Unk	Unk	Fly	4.3															
Enneboeus ovalis	4	1	1	Fac	Unk	Unk	Fly	3.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1

Family-Species Binomial	DS	EMG	ST	Sapro-xylicity	Feeding Guild	Habitat	Dispersal Mode	Body Length	Month of Capture in Emergence Trap														
									M	J	J	A	S	O	N	D	J	F	M	A	M-A	S-D	J-A
Ciidae																								
Ciidae KH sp 01	0	0	1	Obl	Myco	Fungi	Fly	1.1															
Ciidae KH sp 02	0	0	2	Obl	Myco	Fungi	Fly	1.3															
Ciidae KH sp 03	0	0	3	Obl	Myco	Fungi	Fly	1.5															
Ciidae TFIC sp 02	0	0	4	Obl	Myco	Fungi	Fly	1.4															
Ciidae TFIC sp 05	0	0	5	Obl	Myco	Fungi	Fly	1.7															
Melandryidae																								
Callidircaea venusta	0	0	22	Obl	Myco	Unk	Fly	7.7															
Ctenoplectron TFIC sp 01	0	0	1	Obl	Myco	Unk	Fly	6.3															
Melandryidae TFIC sp 03	0	0	3	Obl	Myco	Unk	Fly	2.2															
Melandryidae TFIC sp 04	0	1	1	Obl	Myco	Unk	Fly	2.6	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Mystes planatus	0	0	1	Obl	Myco	Unk	Fly	7.1															
Orchesia ?austrina	0	1	7	Obl	Myco	Rotten	Fly	3.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Orchesia eucalypti	0	0	4	Obl	Myco	Rotten	Fly	3.2															
Orchesia minuta	0	48	35	Obl	Myco	Rotten	Fly	1.6	-	-	-	-	-	-	-	6	15	-	-	-	-	26	1
Orchesia TFIC sp 01	0	0	8	Obl	Myco	Rotten	Fly	3.3															
Orchesia TFIC sp 02	0	0	2	Obl	Myco	G/B Sur.	Fly	3.2															
Mordellidae																								
Mordella promiscua	0	0	3	Obl	Xylo	Unk	Fly	5.6															
Mordellidae KH sp 01	0	0	7	Obl	Xylo	Unk	Fly	3.9															
Mordellidae KH sp 02	0	0	1	Obl	Xylo	Unk	Fly	3.0															
Mordellidae KH sp 03	0	0	1	Obl	Xylo	Unk	Fly	2.9															
Mordellidae KH sp 04	0	0	1	Obl	Xylo	Unk	Fly	3.9															

Family-Species Binomial	DS	EMG	ST	Sapro-xylicity	Feeding Guild	Habitat	Dispersal Mode	Body Length	M	J	J	A	S	O	N	D	J	F	M	A	M-A	S-D	J-A
Mordellidae TFIC sp 03	0	0	20	Obl	Xylo	Unk	Fly	3															
Mordellidae TFIC sp 04	0	0	1	Obl	Xylo	Unk	Fly	2.8															
Rhipiphoridae																							
Rhipiphoridae TFIC sp 01	0	0	1	Obl	Pred	Rotten	Fly	3.1															
Zopheridae																							
Ablabus obscurus	0	0	3	Obl	Xylo	Unk	Fly	3.9															
Docalis funerosus	4	7	2	Obl	Xylo	Bark	Fly	4	-	-	-	1	-	-	1	1	1	-	-	-	1	1	1
Enhypnon tuberculatus	0	1	0	Obl	Xylo	Rotten	Fly	2.5	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Ericmodes australis	0	1	2	Obl	Xylo	Unk	Fly	3.9															
Latometus differens	0	1	20	Obl	Xylo	Bark	Fly	2.7	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Penthelispa fuliginosa	2	5	3	Obl	Xylo	Bark	Fly	3.7	-	-	-	-	-	-	-	-	-	-	-	-	-	2	3
Pycnomerus TFIC sp 02	179	43	80	Obl	Xylo	Rotten	Fly	3.1	1	1	-	-	1	-	1	1	1	3	-	-	-	7	26
Zopheridae KH sp 01	0	0	1	Obl	Xylo	Unk	Fly	4.6															
Zopheridae KH sp 02	0	3	1	Obl	Xylo	Unk	Fly	5.9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3
Tenebrionidae																							
Appelatus tasmanicus	0	1	1	Obl	Sapro	Unk	Fly	6.3	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Brycopia picta	0	1	0	Obl	Xylo	Rotten	Crawl	4.8	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Coripera deplanata	1	0	0	Obl	Xylo	Rotten	Crawl	13															
Diemenoma commoda	0	1	0	Obl	Xylo	Rotten	Crawl	6.7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Diemenoma tasmanica	1	0	0	Obl	Xylo	Rotten	Crawl	8.1															
Isopteron triviale	0	1	0	Obl	Xylo	Unk	Crawl	7.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Meneristes australis	1	0	0	Fac	Sapro	G/B Sur.	Fly	20.1															
Nypsius aeneopiceus	31	2	1	Obl	Sapro	Rotten	Fly	7.9	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-
Olisthaena nitida	0	1	0	Obl	Sapro	Unk	Fly	10.7	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-

Family-Species Binomial	DS	EMG	ST	Sapro-xylicity	Feeding Guild	Habitat	Dispersal Mode	Body Length	M	J	J	A	S	O	N	D	J	F	M	A	M-A	S-D	J-A
Platydema sp nr limacella	0	1	1	Obl	Sapro	Unk	Fly	3.6	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Tenebrioninae TFIC sp 02	1	1	0	Fac	Sapro	G/B Sur.	Fly	7.2	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Prostomidae																							
Dryocora cephalotes	134	11	3	Obl	Xylo	Rotten	Fly	4.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Prostomis atkinsoni	62	9	0	Obl	Xylo	Rotten	Fly	7	-	-	-	-	-	-	-	1	-	-	-	-	-	1	7
Oedemeridae																							
Asclera sublineata	2	2	14	Obl	Pred	Rotten	Fly	3.3	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-
Dohrnia miranda	7	10	3	Obl	Pred	Rotten	Fly	7.9	-	-	-	-	-	-	-	3	2	-	-	-	-	5	-
Dohrnia simplex	0	1	36	Obl	Pred	Rotten	Fly	6.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Oedemeridae KH sp 1	0	1	0	Obl	Pred	Rotten	Fly	2.9	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Oedemeridae TFIC sp 01	0	0	1	Obl	Pred	Rotten	Fly	6.6															
Pseudolycus haemorrhoidalis	1	0	5	Obl	Pred	Rotten	Fly	9.5															
Mycteridae																							
Mycteridae KH sp 01	0	1	1	Obl	Pred	Unk	Fly	2.8	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Trichosalpingus TFIC sp 01	0	9	2	Obl	Pred	Unk	Fly	3.6	-	-	-	-	-	-	-	2	4	2	1	-	-	-	-
Trichosalpingus TFIC sp 02	0	0	10	Obl	Pred	Unk	Fly	3.3															
Trichosalpingus TFIC sp 03	0	0	6	Obl	Pred	Unk	Fly	2.7															
Pyrochroidae																							
Pyrochroidae KH sp 01	0	0	1	Obl	Sapro	Unk	Fly	5.1															
Salpingidae																							
Neosalpingus hybridus	0	0	30	Obl	Pred	Unk	Fly	2.2															
Orphanotrophium frigidum	0	1	11	Obl	Pred	Bark	Fly	2	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Anthicidae																							
Anthicidae KH sp 01	0	2	0	Fac	Pred	G/B Sur.	Fly	2.5	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1

Family-Species Binomial	DS	EMG	ST	Sapro-xylicity	Feeding Guild	Habitat	Dispersal Mode	Body Length	Month of Capture in Emergence Trap															
									M	J	J	A	S	O	N	D	J	F	M	A	M-A	S-D	J-A
Anthicidae TFIC sp 01	0	0	8	Fac	Pred	G/B Sur.	Fly	3.7															
Anthicidae TFIC sp 02	0	0	1	Fac	Pred	G/B Sur.	Fly	1.9															
Aderidae																							
Aderidae KH sp 01	1	9	56	Obl	Sapro	Rotten	Fly	1.8	-	-	-	-	-	-	-	-	4	-	-	-	-	3	2
Aderidae KH sp 02	0	0	2	Obl	Sapro	Rotten	Fly	1.9															
Aderidae TFIC sp 03	0	0	5	Obl	Sapro	Rotten	Fly	2.1															
Scraptiidae																							
Scraptia laticollis	0	50	83	Obl	Sapro	Subcortical	Fly	2.6	-	-	-	-	-	-	2	6	13	1	1	-	-	22	3
Scraptia TFIC sp 01	0	5	4	Obl	Sapro	Subcortical	Fly	3.6	-	-	-	-	-	-	-	-	-	-	-	-	-	4	1
Cerambycidae																							
Ancita marginicollis	0	0	1	Obl	Xylo	Rotten	Fly	5.7															
Callidiopsis scutellaris	5	1	1	Obl	Xylo	Rotten	Fly	17.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Mecynopus cothurnatus	0	0	1	Obl	Xylo	Rotten	Fly	11.1															
Notoceresium TFIC sp 01	0	0	1	Obl	Xylo	Rotten	Fly	4.9															
Stenoderus suturalis	0	0	3	Obl	Xylo	Rotten	Fly	8.3															
Toxeutes arcuatus	7	0	0	Obl	Xylo	Rotten	Fly	41															
Chrysomelidae																							
Aporocera viridis	0	1	1	Fac	Sapro	G/B Sur.	Fly	7.3	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Cryptocephalinae KH sp 01	0	0	1	Fac	Sapro	G/B Sur.	Fly	0.9															
Cryptocephalinae TFIC sp 02	0	0	6	Fac	Sapro	G/B Sur.	Fly	2.2															
Cryptocephalinae TFIC sp 06	0	0	1	Fac	Sapro	G/B Sur.	Fly	6.4															
Anthribidae																							
Anthribidae TFIC sp 01	0	0	5	Fac	Myco	G/B Sur.	Fly	2.1															

Family-Species Binomial	DS	EMG	ST	Sapro-xylicity	Feeding Guild	Habitat	Dispersal Mode	Body Length	M	J	J	A	S	O	N	D	J	F	M	A	MA	S-D	J-A
Anthribidae TFIC sp 04	0	0	4	Fac	Myco	G/B Sur.	Fly	1.6															
Telala? TFIC sp 01	2	0	3	Fac	Myco	G/B Sur.	Fly	3.1															
Xynotropis micans	0	1	0	Obl	Myco	G/B Sur.	Fly	1.9	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Attelabidae																							
Auletobius TFIC sp 01	0	1	5	Fac	Unk	Unk	Fly	1.8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Curculionidae																							
Curculionidae KH sp 01	0	1	0	Fac	Xylo	Unk	Unk	4.7	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Amasa truncata	2	1	1	Obl	Xylo	Rotten	Fly	2.9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Ancyttalia oleariae	0	0	9	Obl	Xylo	Rotten	Fly	4.2															
Ancyttalia tarsalis	0	0	2	Obl	Xylo	Solid wood	Fly	2.2															
Cossonus KH sp 01	26	40	112	Obl	Xylo	Rotten	Fly	2.8	-	-	1	-	-	-	-	-	1	-	2	1	-	2	16
Cossonus simsoni	300	13	34	Obl	Xylo	Rotten	Fly	5.2	-	-	-	-	-	-	-	-	-	-	-	-	-	1	3
Cryptorhynchinae KH sp 01	0	4	0	Obl	Xylo	Rotten	Crawl	1.6	-	-	-	-	-	-	-	1	-	3	-	-	-	-	-
Cryptorhynchinae KH sp 02	0	1	0	Obl	Xylo	Rotten	Crawl	3.9	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Cryptorhynchinae TFIC sp 02	1	1	1	Obl	Xylo	Rotten	Crawl	7.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Cryptorhynchinae TFIC sp 09	0	1	1	Obl	Xylo	Rotten	Crawl	4.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Cryptorhynchinae TFIC sp 11	0	0	1	Obl	Xylo	Rotten	Crawl	2.3															
Curculionidae KH sp 02	0	1	0	Fac	Xylo	Unk	Unk	3.8	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Curculionidae KH sp 05	0	1	1	Fac	Xylo	Unk	Unk	2.4	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Curculionidae KH sp 06	0	0	3	Fac	Xylo	Unk	Unk	2.2															
Curculionidae KH sp 07	0	0	1	Fac	Xylo	Unk	Fly	1.8															
Curculionidae KH sp 08	0	0	1	Fac	Xylo	Unk	Unk	1.9															
Curculionidae KH sp 09	0	0	1	Fac	Xylo	Unk	Unk	2.2															
Curculionidae KH sp 10	0	0	1	Fac	Xylo	Unk	Unk	2.9															

Family-Species Binomial	DS	EMG	ST	Sapro-xylicity	Feeding Guild	Habitat	Dispersal Mode	Body Length	M	J	J	A	S	O	N	D	J	F	M	A	M-A	S-D	J-A
Curculionidae KH sp 12	0	0	1	Fac	Xylo	Unk	Unk	2.2															
Curculionidae KH sp 13	0	0	1	Fac	Xylo	Unk	Unk	2.8															
Curculionidae KH sp 14	0	0	1	Fac	Xylo	Unk	Unk	2.7															
Curculionidae KH sp 15	0	0	1	Fac	Xylo	Unk	Unk	2.7															
Curculionidae KH sp 16	0	0	1	Fac	Xylo	Unk	Unk	2.3															
Curculionidae KH sp 17	0	0	1	Fac	Xylo	Unk	Unk	1.8															
Curculionidae KH sp 18	0	1	0	Fac	Xylo	Unk	Unk	3.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Curculionidae KH sp 19	0	1	0	Fac	Xylo	Unk	Unk	4.1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Curculionidae KH sp 21	0	0	1	Fac	Xylo	Unk	Unk	2.2															
Decilaus lateralis	0	1	0	Obl	Xylo	Subcortical	Crawl	3.3	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Dryophthorus ECZ sp 02	2	0	0	Obl	Xylo	Rotten	Fly	3.3															
Exeiratus TFIC sp 01	0	2	0	Obl	Xylo	Rotten	Crawl	2.5	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-
Exithius capucinus	0	8	1	Obl	Xylo	Rotten	Crawl	5.7	-	-	-	-	1	-	1	-	-	-	-	-	2	3	-
Merimnetes TFIC sp 04	0	1	0	Fac	Unk	G/B Sur.	Fly	2.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Miocallus pygmaeus	0	3	14	Obl	Xylo	Rotten	Crawl	1.1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Pentarthrum TFIC sp 03	60	60	62	Obl	Xylo	Solid wood	Fly	2.8	-	-	-	-	-	-	1	-	1	-	-	-	1	32	22
Perperus TFIC sp 02	1	0	0	Obl	Xylo	Rotten	Fly	5.1															
Platypus subgranosus	1	13	39	Obl	Xylo	Solid wood	Fly	4.1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Poropterus antiquus	0	1	0	Obl	Xylo	Rotten	Crawl	11.5	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Poropterus succisus	0	0	2	Obl	Xylo	Rotten	Crawl	12.1															
Prostomus murinus	1	1	0	Obl	Xylo	Rotten	Fly	19.8	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Roptoperus tasmaniensis	0	1	0	Obl	Xylo	Rotten	Crawl	4	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tychiinae TFIC sp 05	0	0	1	Obl	Xylo	Rotten	Fly	2.3															
Tychiinae TFIC sp 06	0	0	4	Obl	Xylo	Rotten	Fly	2.7															

Family-Species Binomial	DS	EMG	ST	Sapro-xylicity	Feeding Guild	Habitat	Dispersal Mode	Body Length	Month of Capture in Emergence Trap														
									M	J	J	A	S	O	N	D	J	F	M	A	M-A	S-D	J-A
Tychiinae TFIC sp 08	0	1	0	Obl	Unk	Unk	Fly	2.6	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Tyrtaeosus ustulatus	19	20	0	Obl	Xylo	Rotten	Crawl	5	1	-	-	2	-	1	1	-	-	-	1	1	2	9	2
Xyleochinus ?acaciae	0	0	1	Obl	Xylo	Bark	Fly	1.6															

Chapter 4

Comparison and evaluation of techniques to correct species richness for sampling effort

4.1 INTRODUCTION

Conservation of native biodiversity is an important goal of sustainable forestry. In Tasmania, forest biodiversity is conserved through a network of reserves, and within the production forest system. Saproxylic beetles are a diverse, species rich group that are dependent on dead wood (Speight 1989) and on the trees that generate it (Grove 2002c). This makes them potentially vulnerable to forestry, which alters their habitat (Niemelä 1997). To optimise management practices for both conservation and economics, the saproxylic beetle diversity of different forest components, such as trees of different ages needs to be understood.

Older, larger diameter trees and logs have been shown to have a higher species richness of saproxylic invertebrates than younger, smaller diameter wood fractions in many studies (Irmler *et al.* 1996; Kappes and Topp 2004; Kolström and Lumatjärvi 2000; Nilsson and Baranowski 1997; Väisänen *et al.* 1993). Studies on fungal and bryophyte biodiversity have presented similar relationships (Bader *et al.* 1995; Hoiland and Bendiksen 1996; Kruys *et al.* 1999). The validity of these relationships has recently been questioned (Heilmann-Clausen and Christensen 2004; Jonsson *et al.* 2005; Yee 2005). If sampling effort has not been considered adequately, the diameter relationship may just reflect the simple, positive relationship between species richness and area (since volume and surface area are an inherent function of diameter, often a larger amount has been sampled in the larger diameter trees and logs). Recent studies that have considered sampling effort have found smaller diameter wood fractions to be more species rich than similar sized larger diameter fractions and an important habitat for insect and fungal biodiversity (Heilmann-Clausen and Christensen 2004; Kruys and Jonsson 1999; Nordén *et al.* 2004; Schiegg 2001).

Species richness is the simplest way to describe a assemblage's diversity (Gotelli and Colwell 2001) and is commonly used along with species diversity indices to characterise an array of ecological communities (Buddle *et al.* 2005; Condit *et al.*

1996; Hammond 1997; Heilmann-Clausen and Christensen 2004; James and Warner 1982; Lande *et al.* 2000; Loehle *et al.* 2005; Magurran 2004; Schiegg 2001; Sippola and Renvall 1999; Yee 2005). Raw species richness data are particularly vulnerable to sampling effort (Lande *et al.* 2000) and need to be standardised for accurate comparison between different datasets. Various techniques can be used to standardise species richness, with the two most commonly used and recommended techniques being species accumulation curves and rarefaction (Buddle *et al.* 2005; Gotelli and Colwell 2001; Kruys and Jonsson 1999; Lindhe and Lindelöw 2004; Magurran 2004). Species accumulation curves are produced by plotting the cumulative number of species as a function of sampling effort and hence give a record of how many species are collected with an increase in sampling effort (Magurran 2004). Rarefaction uses an algorithm to repeatedly resample individuals or samples from the total dataset to generate a curve of expected species richness against sampling effort (Gotelli and Colwell 2001; Magurran 2004). Species accumulation curves and rarefaction are very closely related; the rarefaction curve can be viewed as the statistical expectation of the accumulation curve with a different reordering of individuals or samples (Gotelli and Colwell 2001). Sampled-based rarefaction curves are often referred to as 'smoothed or randomised species accumulation curves' (Gotelli and Colwell 2001).

Different measures can be used to represent sampling effort for rarefied or accumulation curves. Typically this is the number of individuals (Willott 2001) or area sampled (Condit *et al.* 1996), but can also include number of samples, volume sampled, number of trap days, etc. The measure used for standardisation of sampling effort needs to be appropriate for the dataset and considered carefully as it may alter the result. Heilmann-Clausen's (2004) study of fungal diversity associated with coarse wood debris in Denmark found that when using individual-based rarefaction curves, logs and branches had equal richness, but when comparisons were made by volume-based rarefaction curves branches had a significantly greater richness.

This chapter uses data from emergence trapping of beetles from the stems of living *E. obliqua* trees representing three different age-classes from Tasmanian's wet forests. Species richness for each tree age-class is determined and compared using a variety of methods to adjust for sampling effort. Standardisation of sampling effort

is conducted using different mathematical techniques. Since a tree is a three-dimensional, discrete entity, five different and relevant measures of comparison (Heilmann-Clausen and Christensen 2004) were also used. The sampling effort was standardised by each of these five measures: the number of samples taken; the number of individuals collected; sampled wood volume; sampled wood surface area; and estimated volume of the whole tree.

Several of these methods employed here (such as rarefaction), have been used by various researchers, whilst others are new variations that may be useful for studies with a similar type of data and experimental design. The advantages and disadvantages of the techniques are discussed and recommendations for appropriate comparison of species richness presented.

Species richness is only one component of diversity. A more accurate description of diversity needs to also incorporate the relative abundance of species (evenness) and species composition (Magurran 2004). These measures are also vulnerable to differences in sampling effort. Recommendations of ways to overcome these differences are made.

The data presented are being used as a case study for the evaluation of techniques to standardise sampling effort for the accurate comparison of species richness between datasets. The discussion of the results has been limited to a comparison of techniques only. Explanations of any differences in saproxylic beetle diversity between the age-classes are discussed in detail in the next chapter.

4.3 METHODS

Data Collection

Beetle abundance data were collected by emergence trapping of wood billets cut from the stems of eighteen *E. obliqua* trees (six trees from each of three age-classes: young trees (69 years old); medium-age trees (105 years old); and old trees (> 150 years old). For full details of the study site and sampling methods see Chapter 2.

In summary, eighteen trees were randomly chosen and felled from along two transects. Wood billets were cut from each stem at three standard heights (11m–12 m) above ground-level, immediately below the crown and within the live

crown). Single half-metre long billets were sampled from medium-aged and old trees; and single one-metre long billets were sampled from younger trees. A longer billet was taken for the younger trees to increase the amount of wood sampled, given their small diameter.

The bark was separated from the stem and each billet placed in a separate emergence trap made of fine mesh. Beetle emergence was monitored for eighteen months. All collected beetles were mounted and identified to morphospecies.

Several environmental variables were recorded for each tree (see Chapter 2 for a complete list of variables recorded). The wood volume and surface area of each billet were estimated using the formula for a cylinder:

volume $(cm^3) = \pi r^2 l$

surface area $(cm^2) = 2\pi r l$

where l = length of the wood piece and r is the radius.

Often a truncated cone formula is used to calculate stem or log volume as the radius varies at each end. This was not applicable for these short billets, as the radius at both ends was reasonably consistent.

Data Analysis

Various different manipulation techniques and measures were used to standardise sampling effort for each tree or each tree age-class. Each method is described below. Through out this thesis the term *species richness* is used for both relations between numbers of species and numbers of individuals and *species density* the term used for relations between species number and samples (in this case sections of individual trees), wood volumes and surface areas.

Comparison of species density by pooling of samples to equalise sampled surface area or volume

This approach standardises species density by pooling randomly selected smaller samples (based on the amount of wood sampled for each tree) to equate to the largest sampled volume or sampled surface area. The total species density was then

calculated for each age-class. First, correlation analysis was used to find which variable, sampled volume or sampled surface area was best correlated with species number. This standardising approach is similar to that of Schiegg (2001) and Yee (2005).

a)

b)
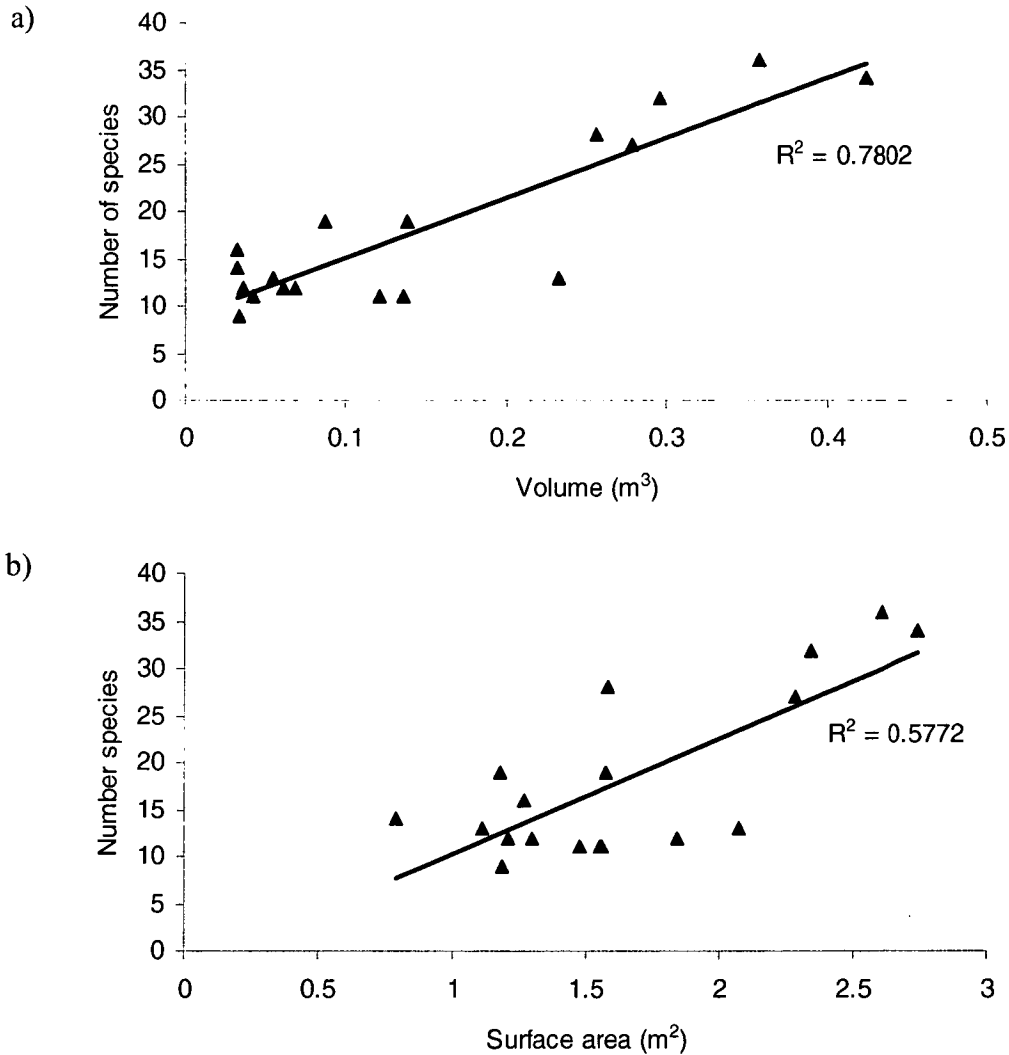
Figure 4.1 Scatterplot and linear regression line of number of saproxylic beetles as a function of (a) volume of tree sampled or (b) surface area of tree sampled.

The number of species collected per tree sample was positively correlated for both sampled wood volume (Pearson's $r^2 = 0.78$, p = 0.000001), Figure 4.1) and sampled surface area (Pearson's $r^2 = 0.58$, p = 0.0003, Figure 4.1). Sampled wood volume had a stronger positive correlation with number of species than did surface area. However, sampled volume from a single tree in the oldest class ($0.308 \ m^3 \pm 0.071$) was just over three times greater than the sampled volume of a tree in the medium-

age-class (0.100 m^3 ± 0.036) and slightly under eight times the sampled volume of a young tree (0.040 m^3 ± 0.011). Therefore, it would require eight of the young trees to match the volume of just one tree from the oldest age-class. This would not allow for any randomisation in tree selection to occur. As surface area also correlated strongly with species number, it was decided to equate sampled surface area.

The sampled surface area of a tree in the oldest age-class (2.27 m^3 ± 0.41) was on average just under two times more than a tree in the medium age-class (1.36 m^3 ± 0.22) and the youngest age-class (1.31 m^3 ± 0.34). To calculate an adjusted total species richness value, the species data for two randomly chosen trees in the youngest age-class were pooled. One older tree with the closest volume (to the total volume of the two randomly chosen younger trees) was then selected. This procedure was repeated until all younger trees were selected. This resulted in all six younger trees been considered and three of the oldest trees. The same procedure was followed to give adjusted totals for the medium-age-class. Adjusted species richness for sampled surface area was compared between each age-class using a one-way analysis of variance (ANOVA) using SAS 9.1(Anon. 2002) and a follow up multiple comparison test (Ryan-Einot-Gabriel-Welsch Multiple Range Test: REGW test).

Comparison of species density by random sub-sampling of the dataset to equalise volume or surface area

A reduction factor was calculated for each tree to equalise sampled volumes to the smallest sampled volume. This factor was then used to calculate the expected number of individuals for each tree if the sampled volume were equal (i.e. Tree *n* volume/smallest tree volume X Tree *n* number of individuals). Adjusted species number was then determined by randomly selecting the reduced number of individuals from the complete dataset for each tree. The random selection of individuals from the complete dataset was repeated ten times to obtain an 'average' species list for each tree. The data were collated and total number of species for each age-class was determined. Adjusted species densities for sampled volume and sampled surface area were compared between each age-class using one-way

analyses of variance (ANOVA) using SAS 9.1 (Anon. 2002) and a follow up multiple comparison test (Ryan-Einot-Gabriel-Welsch Multiple Range Test: REGW test).

Taxon Sampling Curves

Taxon sampling curves such as rarefaction or species accumulation curves are becoming increasingly used (Grove 2000; Hammond *et al.* 2001; Wikars *et al.* 2005) and recommended as a standard technique to compare species richness across datasets with varying sampling effort (Buddle *et al.* 2005; Gotelli and Colwell 2001; Magurran 2004). Forms of rarefaction have been in use since first proposed in Sanders' (1968) original paper. The original formula has been modified by Hulbert (1971) and Simberloff (1979). Coleman (1981; 1982) introduced the 'random placement method.' This technique uses a different approach that is much more efficient to calculate and produces virtually indistinguishable results (Colwell and Coddington 1994; Gotelli and Colwell 2001). As rarefaction curves are calculated by repeated resampling of the total dataset, estimates of variance are possible, allowing easier comparison of different datasets than the traditional species accumulation curves (Buddle *et al.* 2005).

A significant problem exists with classical and Coleman rarefaction, where biased results can be obtained if the samples are drawn from datasets with markedly different abundance distributions (Fager 1972; Gray 2000; Magurran 2004). If a sample is homogenous with similar distributions of individuals among species it will have a steeper initial slope than a sample where the distribution of individuals is highly uneven with a few species having many more individuals than others (Figure 4.2), even though the overall species richness is the same. When the samples are compared before the total number of species is reached, the species richness of the two samples could be considered to be significantly different. Smaller sample sizes exacerbate this, for example in Figure 4.2 if only 100 individuals are sampled the expected species richness can vary between 7 species (uneven abundance distribution) and 32 species (even abundance distribution). The calculation of rarefaction also assumes that a species distribution is random. In nature random distributions are rare and most species have aggregated distributions

(Williams 1964). With higher levels of aggregation, rarefaction increasingly tends to overestimate the actual species richness (Fager 1972; Gray 2000). This is also exacerbated at a smaller sample size (Simberloff 1978). As both the individual-based Coleman and classical rarefaction methods make these two assumptions they tend to overestimate species richness. A new sample-based rarefaction technique (Mao-Tau) has been developed by Colwell (2004). This moment-based technique overcomes the biases of the classical and Coleman rarefaction and is the rarefaction technique chosen to analyse this dataset.
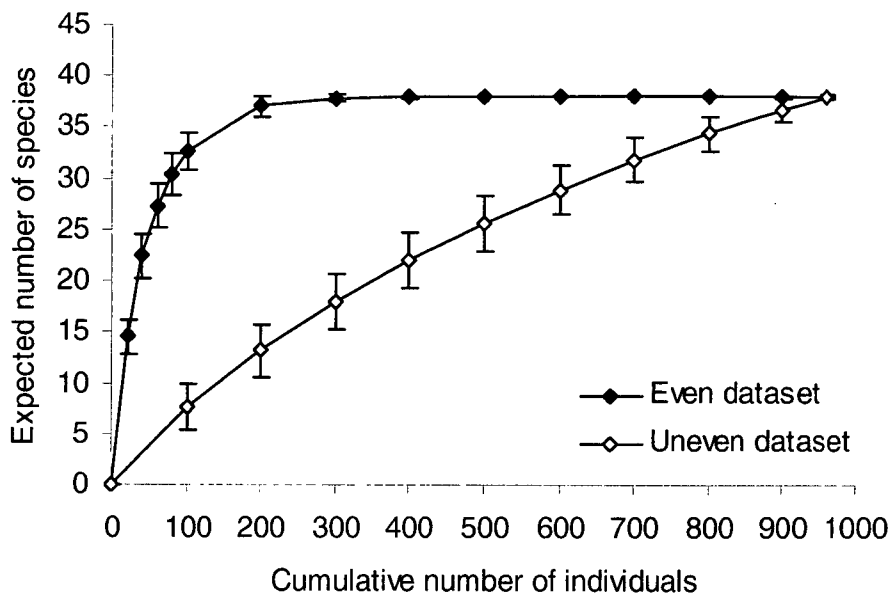
Figure 4.2 Coleman rarefaction curves for two hypothetical datasets. One has an even abundance distribution with all 38 species having the same abundance; the other has an uneven abundance distribution where 37 species have one individual and one species has 892 individuals. This example shows that although both samples have the same total species richness, if the rarefaction curves are compared at a smaller number of individuals, the even dataset appears to be significantly more species rich. (After Fager (1972) and Gray (2000)).

Species diversity for each age-class was evaluated by comparison of Mao-Tau rarefaction curves (Colwell *et al.* 2004) calculated using *EstimateS* Version 7.5 (Colwell 2005). Mao-Tau rarefaction curves with 95% confidence intervals were produced to compare species diversity for each age-class with: 1) equal number of trees; 2) equal number of individuals; 3) equal wood volumes; and 4) equal wood surface area; by rescaling of the x-axis with the appropriate metric. The mean number of individuals for each sample size was calculated using *EstimateS* Version

7.5 (Colwell 2005). The mean sampled volume or sampled surface area for each tree was calculated for each age-class. The cumulative value (surface area or volume) was then plotted against the number of species calculated by *EstimateS* Version 7.5 (Colwell 2005).

Species were divided into two groups, obligate or facultative saproxylic species, based on their dependence on dead wood. Obligate saproxylic species require dead wood or another species that is dead wood dependent to complete their lifecycle (Speight 1989). Facultative species regularly utilise dead wood as part of their lifecycle but this can be interchanged with other similar substrates such as leaf-litter and soil/humus layer. Mao-Tau rarefaction curves based on these two groups were produced to investigate if there was any pattern of preference for a tree age-class.

Species were also divided into two broad groups depending on the location of their preferred habitat. Species were classed as either wood inhabiting (solid or rotten) or surface dwelling (including subcortical species). Patterns for each tree age-class were evaluated using Mao-Tau curves.

Extrapolation to the volume of the whole tree

Rarefaction curves were produced using the online rarefaction calculator (Brzustowski 2002) for each individual tree. This calculator uses the classical formula for rarefaction but can produce a rarefaction curve for a single sample unlike the sample-based Mao Tau method. The total volume for each tree was calculated using the Farm Forestry Toolbox (Anon. 2003) using the specific model developed for *E. obliqua*. The number of individuals expected in this larger volume was calculated by: [(total volume of tree/actual volume sampled) x number of individuals in actual volume sampled]. The rarefaction curves were extrapolated to this total expected number of individuals using four different models. All models are outlined by Melo (2003). Three of these models are curve fitting models: Logarithmic, Exponential and Clench, which were first described by Soberon (1993). The other model, the ECB (termed by Melo (2003)) estimator described by Evans (1955), is based on simple computations. This model does not require the fitting of a non-linear regression model and is simple to calculate using a formula based on the number of sample units and number of species found:

$$S= \frac{s \log(N+1)}{\log(n+1)}$$

where S is the estimated species richness expected to occur in N unit samples and s is the number of observed species in n unit samples.

The mean number of expected species for each model per age-class was calculated and any significant difference in means tested using a one-way analysis of variance (ANOVA) using SAS 9.1 (Anon. 2002). For graphical comparison, extrapolated rarefaction curves for each age-class were calculated using the ECB model. Curves were extrapolated to the average number of species for each age-class at tree total volume.

It was not possible to extrapolate the rarefaction curves for total tree surface area as not all the required measurements where taken during sampling. The total tree volume calculation was possible as a model was already available which only needed two measurements; tree height and diameter at breast height over bark (DBHOB).

4.2 RESULTS

Comparison of species richness with raw data

When unmodified data are compared, the oldest age-class supported the greatest total number of species and mean number of species; followed by the medium age-class and the youngest age-class (Figure 4.3).

Comparison of species density by pooling of wood samples to equalise sampled surface area

The oldest age-class had the largest number of species after standardizing (60 species) for sampled surface area (standardised surface area 7.4 m^2). The medium age-class had slightly more species (44 species; standardised surface area 8.1 m^2) than the youngest age-class (38 species; standardised surface area 7.9 m^2).
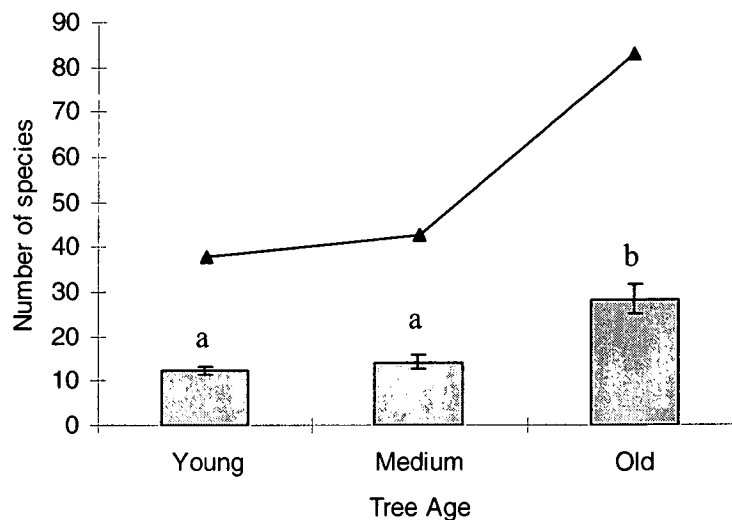
Figure 4.3 Mean (bar) and total (line) number of saproxylic beetle species for each age-class. Error bars show standard error, letters a and b represent significantly different (p<0.05) means from ANOVA.

Comparison of species density by random sub-sampling of dataset to equalise volume or surface area

When species density was compared between tree age-classes using this standardisation technique the results varied notably depending on whether volume or surface area was equalised (Figure 4.4). If volume was equalised (standardised

volume 0.20 m^3 per age-class), the youngest age-class supported a significantly higher number of species than the two older age-classes (Figure 4.4a). This pattern is reversed when standardising by surface area (4.7 m^2 per age-class) with the oldest age-class having significantly more species than the other two age-classes (Figure 4.4b).

a)

b)
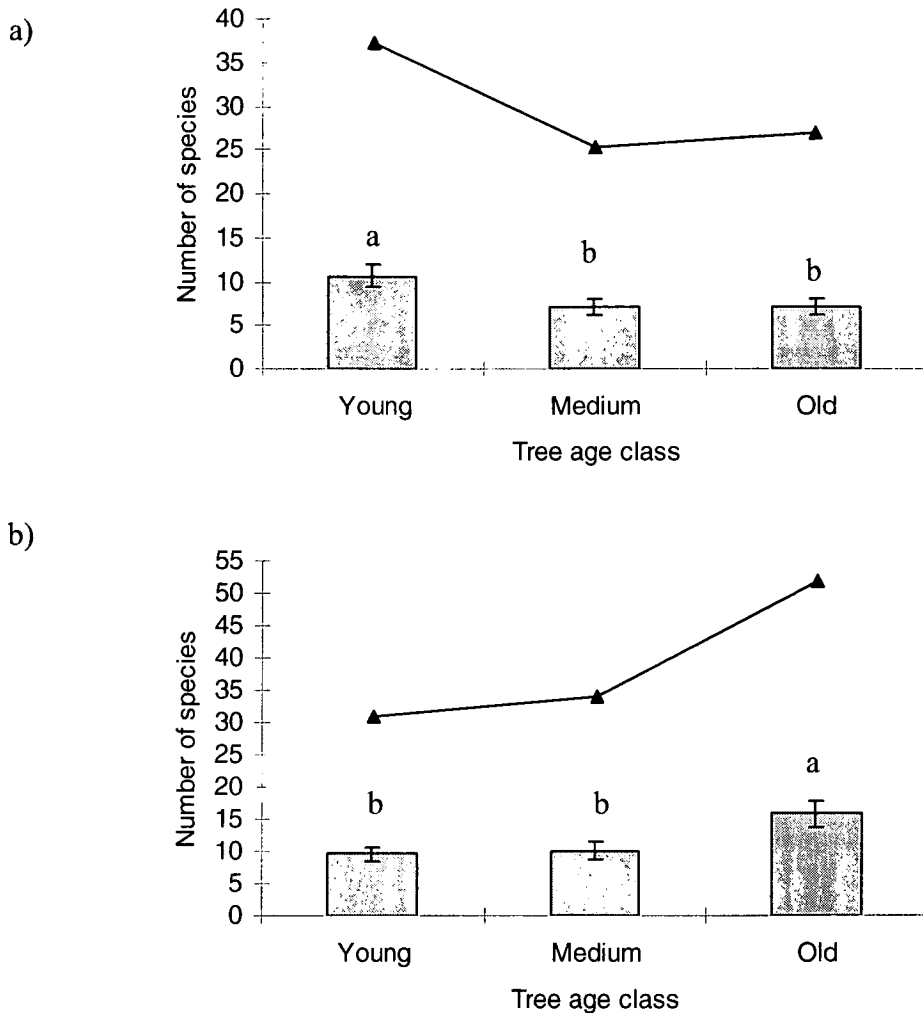
Figure 4.4 Mean (bar) and total (line) number of saproxylic beetle species adjusted by random sub sampling of individuals to equalise either volume (a) or surface area (b) for each age-class. Error bars show standard error, letters a and b represent significantly different (p<0.05) means from ANOVA.

Comparison of species richness and density by Mao-Tau rarefaction

Rarefaction curves based on the number of trees sampled showed the older trees to be significantly more species dense than the two younger age-classes (Figure 4.5a). This is also seen for obligate saproxylic species (Figure 4.5c). The same trend is seen for facultative species but the result is no longer significant (Figure 4.5b).
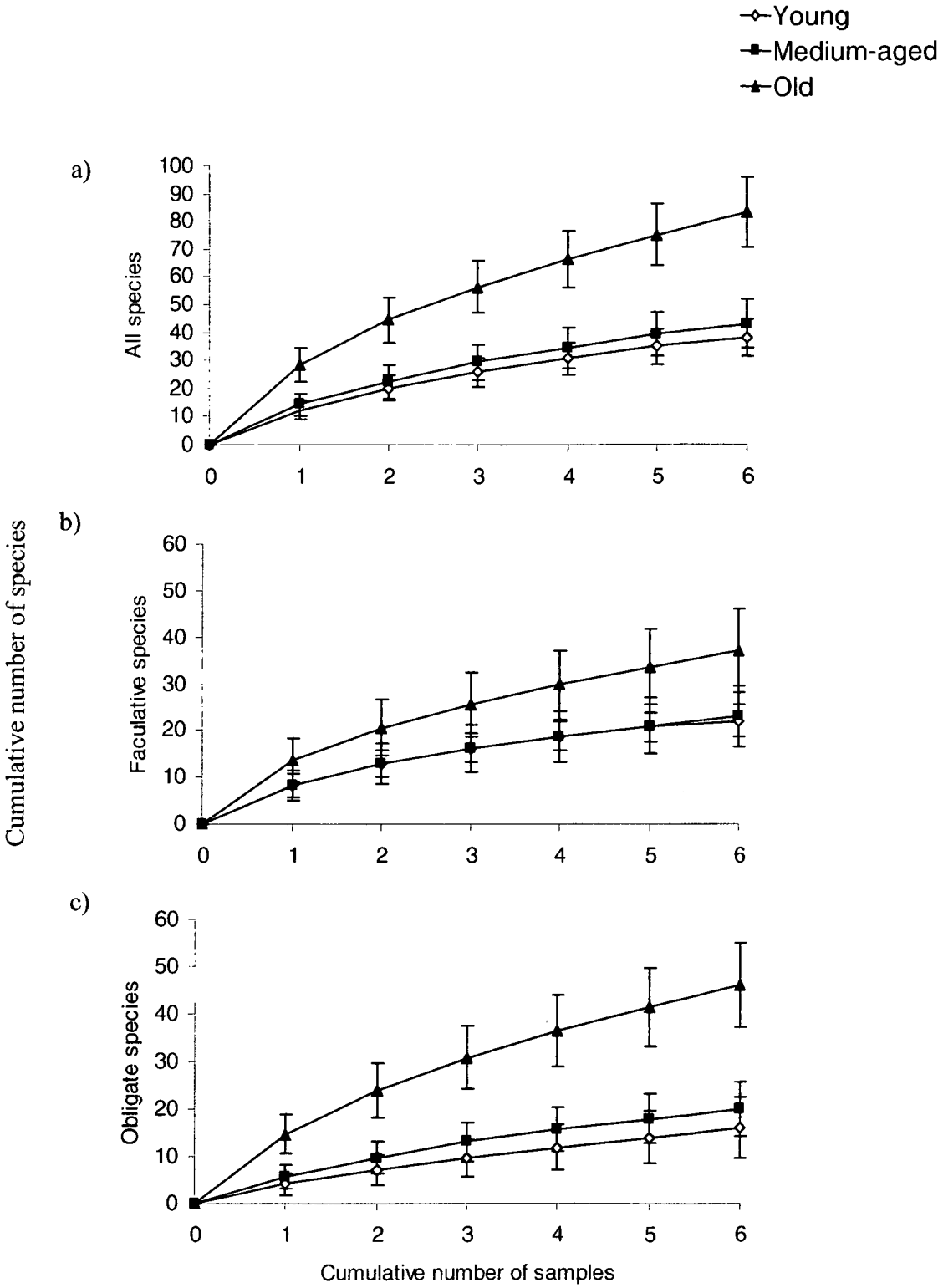
Figure 4.5 Mao-Tau rarefaction curves based on number of trees sampled for all species (a), facultative species (b) and obligate species (c). Note the axes are different scales.

The ranking of tree age-class species richness and density varied with the measure used to produce the rarefaction curve (Figures 4.6 a, d and g). Individual and volume based rarefaction curves show the same trend, with the young trees having the greatest species richness (Figure 4.6a) and species density (Figure 4.6d). This is significant for the volume-based rarefaction curve (Figure 4.6d). The two older tree age-classes had almost equal species richness (Figure 4.6a) and species density based on volume (Figure 4.6d).

Comparisons of rarefaction curves based on surface area show the opposite result with the old trees having a significantly greater species density than the two younger age-classes (Figure 4.6g). The young and medium age trees had a poorer but similar species density.

The curves for facultative species showed the same trend as all species pooled for rarefaction based on individuals, volume and surface area (Figures 4.6b, e and h). A significant difference exists between the curves for young and old trees based on individuals and volume (Figures 4.6c and d). All age-classes have a similar specis density based on surface area (Figures 4.6h). For obligate species the results were similar to that obtained for all species. The difference in species density based on volume for all species was less pronounced and the difference in species density based on surface area was greater than for all species.
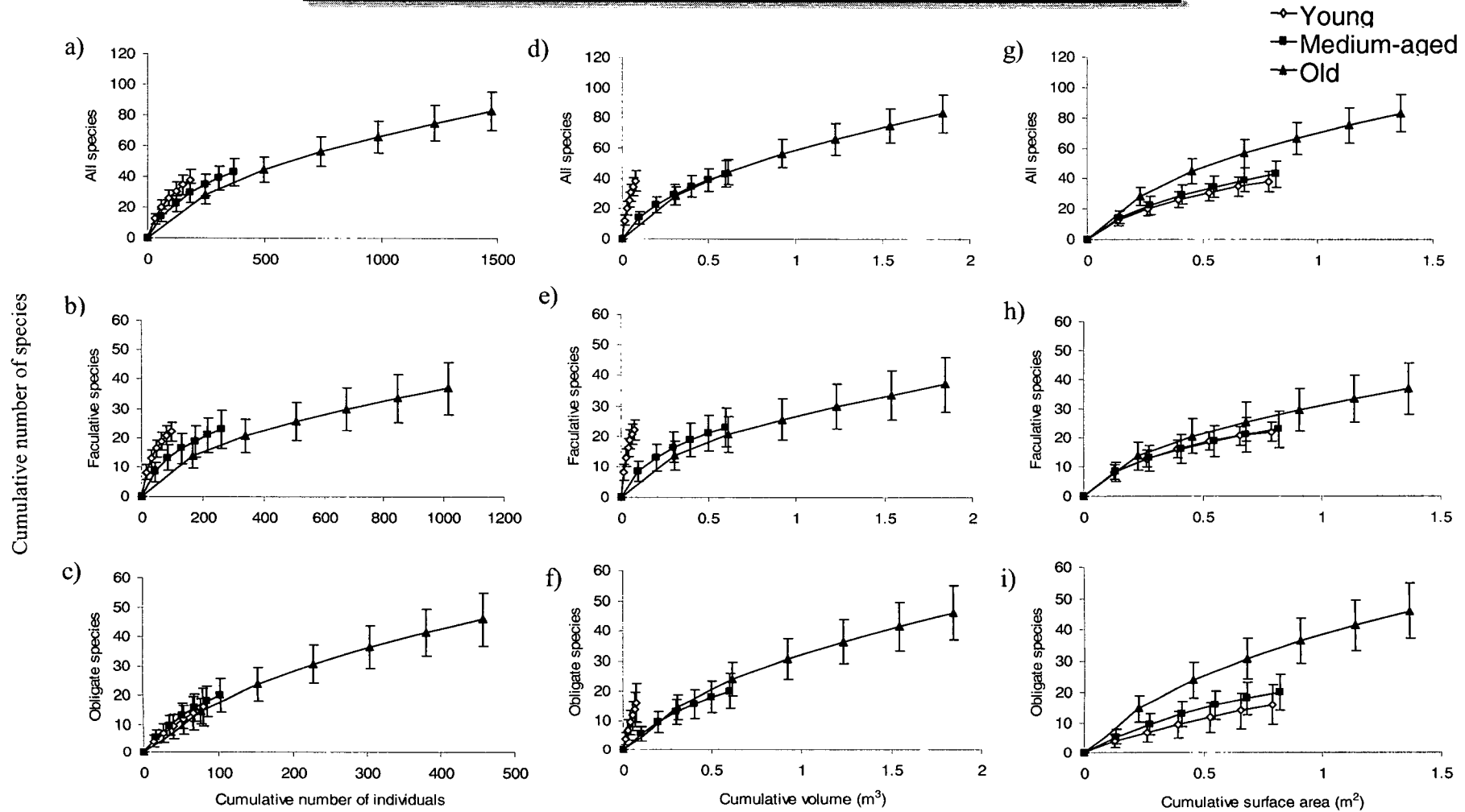
Figure 4.6 Mao-Tau rarefaction curves based on number of individuals sampled (a-c), volume (d-f) and surface area (g-h) for all species (a,d,g), facultative species (b,e,f) and obligate species (c,f,i). Note the axes are different scales.
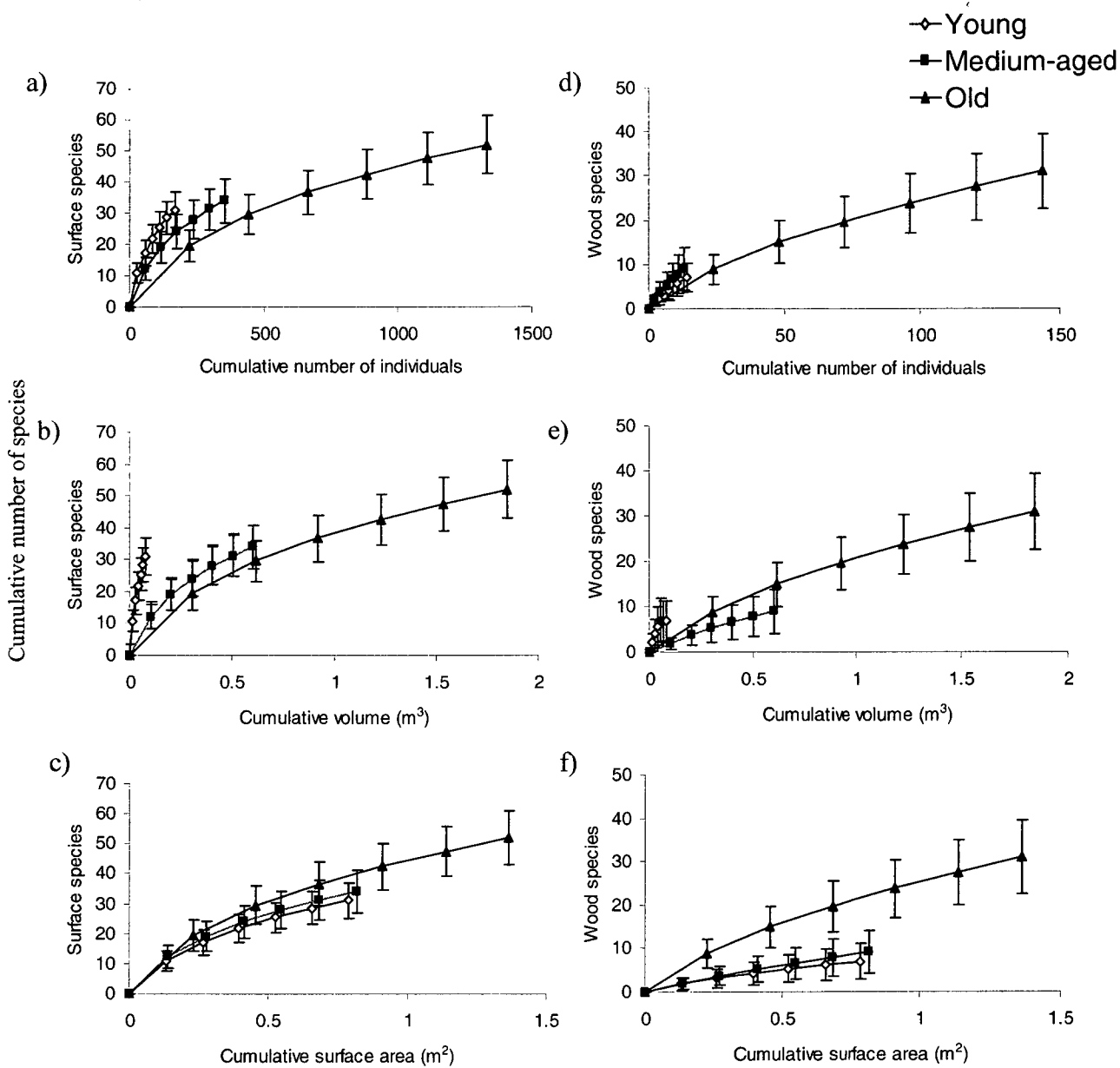
Figure 4.7 Mao-Tau rarefaction curves based on number of individuals sampled (a and d), volume (b and e) and surface area (c and f) for surface and subcortical dwelling species (a-c) and wood dwelling species (d-f). Note the axes are different scales.

The species richness and density for surface-dwelling species shows the same trends as facultative species, with the younger trees having a significantly higher density per volume than the older two age-classes (Figure 4.7a and b). The species density per surface area is not significantly different between age-classes (Figure 4.7c). The wood-dwelling species show a similar ranking of the age-classes (Figure 4.7d, e and f) to the obligate species, with the only difference being that the ranking of age-classes based on volume is no longer significantly different (Figure 4.7e).

Comparison of species richness by extrapolation to equalise volume of whole tree

Table 4.1 Extrapolated species richness using four different models to estimate total species richness per tree. Mean estimated species richness and standard error for each age-class are also shown. Letters a and b represent significant difference in means from ANOVA (p < 0.001) for age-class per model.

Age-class-Tree Code	Actual Species Richness	Expected Tree Species Richness			
	Raw Data from Tree Samples	Exponential model	Clench model	ECB estimator	Logarithmic model
Young					
T7	9	10.5	15.0	17.8	25.5
T9	11	13.4	18.7	19.2	26.9
T24	14	15.4	21.4	24.8	33.9
T25	12	19.4	29.0	22.4	40.9
T41	16	21.9	29.6	24.4	37.8
T43	12	14.5	19.9	19.1	26.9
Mean	**12.3 ± 1.0** [b]	**15.9 ± 1.7** [b]	**22.3 ± 2.4** [b]	**21.3 ± 1.2** [b]	**32.0 ± 2.7** [b]
Medium-aged	19	21.2	30.1	32.9	52.5
T2	19	23.4	33.7	32.9	57.8
T3	12	13.9	19.7	21.2	30.8
T10	13	17.4	26.1	25.4	42.1
T30	11	13.0	19.1	20.2	31.0
T40	11	11.8	16.8	21.2	28.7
T42	**14.2 ± 1.6** [b]	**16.8 ± 1.9** [b]	**24.3 ± 2.8** [b]	**25.6 ± 2.4** [b]	**40.5 ± 5.1** [b]
Mean					
Old					
T4	34	33.6	42.8	48.0	66.0
T5	32	37.6	53.7	50.8	86.9
T6	13	15.8	22.6	22.3	34.6
T21	28	35.1	51.6	50.0	88.1
T44	27	33.6	43.4	42.2	71.5
T45	36	40.2	56.2	58.4	92.1
Mean	**28.3 ± 3.4** [a]	**32.6 ± 3.5** [a]	**45.0 ± 5.0** [a]	**45.3 ± 5.1** [a]	**73.2 ± 8.8** [a]

All models calculated different values of expected species richness for each tree and mean expected richness for each age-class (Table 4.1). The exponential models expected number of species was low and similar to the actual number of species from the sampled volume of tree. In contrast, the logarithmic model predicted species richness to be significantly higher than all other models. The clench model and ECB estimator calculated virtually identical species richness estimates. (This was confirmed by plotting predicted values from each model against each other. The result was a straight line with a slope not far from 1.0.)

When comparing mean values of expected species richness for each age-class, the ranking of the results is (extremely) consistent, irrespective of which of the four models is used (Table 4.1). The oldest age-class always has significantly higher species richness than the younger two age-classes. The two younger age-classes do not have significantly different means, but always follow the same pattern with the medium age-class having a higher species richness value.
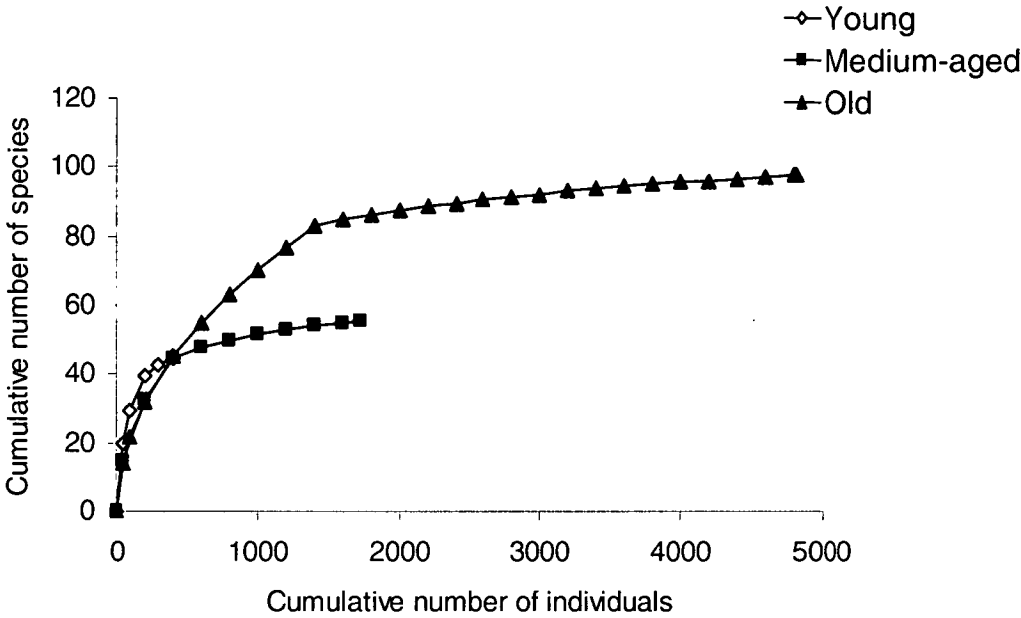
Figure 4.8 Extrapolated rarefaction curves using the ECB estimator to estimate the number of species for the calculated number of individuals in the mean total tree volume of each age-class.

The shapes of the extrapolated rarefaction curves for all age-classes suggest that they are close to reaching an asymptote (e.g. Figure 4.8 shows ECB). The younger age-class has a steeper initial rise than the other two age-classes, but has the lowest expected species richness.

Table 4.2 Summary of richness ranking for each age-class (based on significant difference) , using different techniques and measures to standardise species richness for sampling effort. The age-class with the highest species richness for each technique and measure is highlighted in bold.

		Young Species richness	Medium Species richness	Old Species richness
Raw Data		Equal 2nd	Equal 2nd	**1st**
Pooling				
	Surface area	Equal 2nd	Equal 2nd	**1st**
Random subset				
	Volume	**1st**	Equal 2nd	Equal 2nd
	Surface area	Equal 2nd	Equal 2nd	**1st**
Rarefaction				
All species	*Trees*	Equal 2nd	Equal 2nd	**1st**
	Individuals	**All equal**	**All equal**	**All equal**
	Volume	**1st**	Equal 2nd	Equal 2nd
	Surface area	Equal 2nd	Equal 2nd	**1st**
Facultative species	*Trees*	**All equal**	**All equal**	**All equal**
	Individuals	**1st**	Equal 1st and 2nd	Equal 2nd
	Volume	**1st**	Equal 2nd	Equal 2nd
	Surface area	Equal 2nd	Equal 2nd	**1st**
Obligate species	*Trees*	Equal 2nd	Equal 2nd	**1st**
	Individuals	**All equal**	**All equal**	**All equal**
	Volume	**1st**	Equal 2nd	Equal 2nd
	Surface area	Equal 2nd	Equal 2nd	**1st**
Surface species	*Individuals*	**All equal**	**All equal**	**All equal**
	Volume	**1st**	Equal 2nd	Equal 2nd
	Surface area	**All equal**	**All equal**	**All equal**
Wood species	*Individuals*	**All equal**	**All equal**	**All equal**
	Volume	**All equal**	**All equal**	**All equal**
	Surface area	Equal 2nd	Equal 2nd	**1st**
Extrapolation	*Whole Tree*	Equal 2nd	Equal 2nd	**1st**

Richness ranking was consistent with techniques using the same dataset and metric, except for extrapolation, which does not standardise samples to the same size or effort but to total size for each tree (Table 4.2).

4.4 DISCUSSION

Which technique for standardisation?

The technique used for standardising species richness for this dataset was not as important to the richness ranking of age-class as the metric used. All techniques that used the same measure, except for extrapolation, produced the same diversity ranking for the three age-classes. The actual numerical value of species richness did change depending on the technique applied, generally because each technique compared species richness at different sample sizes. Most researchers use only one technique to standardise sampling effort, so it is difficult to say if this finding is indicative of other datasets. Yee (2005) did use a variety of sampling effort standardizing methods when comparing her dataset of beetles in large and small diameter logs. Only two of these methods, the pooling of samples and cumulative species richness, used the same metric (surface area). The trends for each method were similar, with the smaller diameter logs more species-rich (although not significantly) than large diameter logs. Different metrics did produce different rankings of large and small diameter logs.

The technique of pooling samples to equalise volume or surface area has not been widely used by researchers. Schiegg (2001) used this technique when comparing saproxylic beetles from tree limbs and branches and Yee (2005) used it to compare saproxylic beetles in large and small logs. One limitation of this method is when applying it to a small number of samples. As demonstrated with this dataset, it was not possible to equalise trees by volume even though the correlation was stronger, due to the great disparity in sample volume between young and old. Other limitations of this method are the simplified single figure result which may reduce the level of information obtained (compared with techniques such as rarefaction curves); the computation may become quite cumbersome with a large dataset; and the corrected metric (i.e. surface area or volume) is not exactly equal for each habitat variable. Yee (2005) found after applying this pooling standardisation technique that the mean sampled surface area of smaller diameter logs was still significantly different from that of larger diameter logs. The corrected surface area varied (although not significantly) for different age-classes with the current dataset also.

Standardisation of sampling effort by random sub-sampling of the dataset has little mention in the literature. The modification of abundance data to equalise sampling effort by a simple ratio reduction has been used by various researchers (Buddle *et al.* 2005; Hammond *et al.* 2004; Hooper 1995; Jonsell and Weslien 2003; Kappes and Topp 2004), but the additional component in this technique of randomly selecting the calculated number of individuals from the complete dataset to obtain a species total has not been found elsewhere. The random sub-sampling technique produces the same ranking of age-classes as the pooling of samples and rarefaction, but the value for species richness is quite different. One reason for this is that the standardised surface area is smaller and exactly equal for each age-class, as each tree's surface area is reduced to the smallest sampled surface area. This technique uses a simple calculation to reduce the number of individuals; it assumes a linear relationship between the number of individuals and either volume or surface area. While this relationship is not strictly correct, several researchers have applied it to alter abundance data (Buddle *et al.* 2005; Hooper 1995; Kappes and Topp 2004). The fitting and use of a non-linear model may improve the accuracy of this interpolation step. The randomisation component of this technique is quite slow and tedious to calculate even when using computational tools such as macros to replicate steps and pivot tables to collate the data. It would also be improved by increasing the number of replications. The main advantage of this technique is the randomly selected reduced species list that is generated. This can be used to compare other facets of diversity such as species composition or relative abundance, which are also vulnerable to differences in sampling effort. This is discussed in detail in the following section.

The comparison of taxon sampling curves such as rarefaction or species accumulation curves is commonly recommended to compare species richness or species density across datasets with varying sampling effort (Buddle *et al.* 2005; Colwell *et al.* 2004; Gotelli and Colwell 2001; Magurran 2004). A crucial advantage of rarefaction curves over species accumulation curves is the ability to calculate confidence intervals. Rarefaction curves are easy and rapid to generate, with freely available software such as EstimateS (Colwell 2005). The actual curve provides additional information about a dataset. The rate of accumulation of new species is readily apparent in the shape of the curve, making it possible to determine

if enough samples have been taken to adequately sample a population. In the current dataset, no age-class has reached an asymptote with the existing sampling effort.

Several different methods of rarefaction exist and it is important to be aware of the distinction between them and the assumptions each method makes. While marine literature has recognised the limitations of classical and Coleman rarefaction (Gray 2000) it does not seem to be considered in current arthropod (Buddle *et al.* 2005; Hammond *et al.* 2004; Yee 2005) or fungal literature (Heilmann-Clausen and Christensen 2004). The assumption of heterogeneity of abundance is particularly important when comparing organisms such as invertebrates or benthic fauna where large differences in the abundance of species are likely and a complete or near complete inventory of species is difficult to achieve (Didham *et al.* 1998; Kim 1993). The newly developed sample-based rarefaction technique Mao-Tau described by Colwell, overcomes these assumptions and is applicable to a wide range of taxa with varying relative abundances and distribution patterns. As long as the data are not inherently individual-based it can be analysed using this technique. The sample-based Mao-Tao computation does not require samples to be of the same size or effort (Colwell pers. comm.) as incorrectly stated by Buddle (2005). If the data are obtained from samples with differing sampling effort, the number of species should be plotted as a function of the accumulated number of individuals, not accumulated number of samples, as it is the individual that acts as the replicate (Colwell *et al.* 2004; Gotelli and Colwell 2001).

As rarefaction curves are rapid to generate, different components of a dataset can be readily investigated. For example, Heilmann-Clausen and Christensen (2004) examined the habitat associations of red-listed fungal species (threatened species) by producing separate rarefaction curves for red-listed and non-red-listed species. Relationships between age-class and obligate or facultative saproxylic beetle species and age-class and habitat were investigated in the current study. Both species richness and species density relationships can also be easily explored by overlaying different metrics such as the number of samples, number of individuals, sampled volume or sampled surface area.

All the techniques to standardise data for sampling effort discussed so far have been interpolating techniques, i.e. they compare species richness or density at the smallest sample size. This approach has been criticised due to the loss of

information contained in the larger samples (Elphick 1997; Magurran 2004; Melo *et al.* 2003). A way of solving this problem is to extrapolate the smaller samples to produce expected species richness at the size of the largest sample or at the size of a chosen ecologically significant unit (such as the whole tree). This approach has received little attention from ecologists but several researchers have devised and evaluated extrapolation methods (Evans *et al.* 1955; Keating and Quinn 1998; Melo *et al.* 2003; Soberon and Llorente 1993; Stout and Vandermeer 1975; Tackaberry *et al.* 1997). Different extrapolation models produced different species richness values at the scale of the whole tree. It was not considered correct to apply normal goodness-of-fit procedures to these models to test which one is the most accurate for this dataset as the models were calculated from the rarefaction curve, not from raw species data (Ratkowsky, pers. comm.) However, the logarithmic model is not recommended, as it is a non-asymptotic model: as N goes to infinity, so will the expected species richness. The Clench model and ECB produced virtually identical results for this dataset, with the ECB being the preferred model as it can be calculated simply and does not require any nonlinear regression modelling.

Which metric for standardisation?

The appropriate metric for standardisation needs to be relevant for both conservation and commercial management of the forest. Analysis of this dataset has revealed conflicting ranking of tree age-classes depending on the metric used. Individual-based rarefaction curves indicate that all trees are equally species rich. Both volume-based rarefaction and random sampling techniques show younger trees to be significantly more species-dense. Three techniques to equalise surface area (pooling of samples, random sampling and rarefaction) show the oldest trees to be the most species-dense. This finding is the same as obtained for the raw data, rarefaction based on the number of samples and extrapolation to the whole tree. This variation of results, depending on the metric used when comparing rarefaction curves has been noted previously in studies of fungal diversity of beech trees in Denmark (Heilmann-Clausen and Christensen 2004). Unlike this study, in the Danish study the same ranking pattern was found for both volume and surface area based rarefaction curves.

Species density is considered a more appropriate metric for conservation purposes than species richness as it relates the number of species on a scale relevant to management (Gotelli and Colwell 2001; Heilmann-Clausen and Christensen 2004). Three metrics produced species density- either per sample, per volume or per surface area, and could be applicable for practical conservation tools.

Other researchers (Heilmann-Clausen and Christensen 2004; Lindhe and Lindelöw 2004; Moreno and Halffter 2000; Wikars *et al.* 2005) have used the sample-based metric. However, if the data had been derived from samples with different sampling effort it is vulnerable to the same bias as raw data where a higher species density may be due to a larger sample having been studied (Willott 2001). Therefore, this metric is not recommended to compare this and other datasets with varying sampling effort.

To choose the most appropriate metric (from either surface area or volume) it is necessary to understand why the results vary between these two metrics. First, the smaller diameter trees (younger age trees) have a higher surface area to volume ratio. With doubling in tree diameter, the surface area increases two-fold and the volume increases four-fold. For this reason, the sampled surface area between all three-age-classes is quite similar and the sampled volume is much less so, particularly between the youngest and oldest trees. Second, the majority of species for all age-classes are surface dwelling (including subcortical layer) species and hence tree surface area would better reflect this relationship than tree volume. This explains why rarefaction curves for all tree age-classes have a similar species density based on surface-area for surface-dwelling species and older trees have a significantly higher density for the complimentary rarefaction curve for wood dwelling species. This also explains why the volume-based rarefaction curves show the youngest trees to be more species dense, as the older trees have a much greater volume. If the older trees did not have such a large number of wood dwelling species then the difference in species density for older and younger trees would be even more pronounced.

The richness ranking of the age-classes based on surface area remains consistent; whether by interpolating to the smallest sampled area or extrapolating to compare diversity at the whole tree level (these data are not presented as they were calculated using estimated values for variables not recorded i.e. diameter of stem at tree base

and at tree total height). Inconsistent results are seen when using volume, with a higher diversity in the younger age-class when comparing at the smallest sample size and a higher diversity in the older age-classes when comparing at the whole tree level. Species density at the tree level is a much more intuitive scale to understand than is a density for a certain surface area or volume. When one considers that a younger tree has a higher species density per unit volume than an older tree, it is easy to overlook that an older tree has a much greater volume and therefore a higher overall number of species. As the species density ranking is consistent at both scales for surface area, the same 'intuitive' result is achieved at both scales (smallest sampled surface area or whole tree).

Considering these reasons, surface area would be a better metric, from an ecological perspective, than would volume for the study of invertebrates associated with living trees, as it more appropriately reflects the species density relationship for both surface and wood dwelling species. Heilmann-Clausen (2004) also concluded that surface area was the best predictor of fungal species density across different habitats.

While surface area is a better metric in an ecological context it is not a metric commonly used in forest management. Volume is currently much easier to calculate with programs such as the Farm Forestry Toolbox (Anon. 2003) developed to accurately model volume for different tree species. Only two readily measured inputs (DBHOB and tree height) are required. It may be possible to alter these programs to calculate surface area with the same inputs, allowing surface area to be a more accessible metric for management. Alternatively, if volume is the metric used, it is recommended that the whole tree scale (obtained using extrapolation models) be considered as it more intuitively reflects the number of species associated with trees of varying ages as it takes into account actual tree size.

Species richness as a measure of diversity

Species richness or species density is the most commonly used measure to describe the diversity of different habitats (Lande *et al.* 2000; Magurran 2004). This measure is often used to rank habitats, where a habitat with the highest richness or density is

considered to have higher conservation value. Species richness however, is only one component of diversity. A more complete measure of diversity should include the relative abundance of each species (evenness) (Magurran 2004) and species composition (the identity of each species). The relative abundance of species is often considered along with species richness as a part of a heterogeneity diversity index such as Simpson's index and the Shannon-Wiener index. Diversity indices have received a large amount of criticism, as they produce a non-intuitive single figure value and have been associated with many biases (Buddle *et al.* 2005; Washington 1984). Most diversity indexes are also sample size dependent (Condit *et al.* 1996; Magurran 2004). Some researchers have suggested that diversity indices no longer be used for comparing arthropod biodiversity across habitats (Buddle *et al.* 2005). Species diversity that incorporates richness and relative abundance may be better compared visually through a rank abundance diagram (Magurran 2004; Yee 2005) or by comparing the shape of rarefaction curves as described by Olszewski (2004) which have already been adjusted for sampling effort.

Comparing habitats by species richness or density alone without considering species composition may not produce the best conclusion for conservation. Consider three habitats (such as trees of different ages, as in this study) with varying species richness; is it suitable to conclude that retaining only the more species rich age-class is appropriate for the best conservation outcome? What about the species associated with these different aged trees? If they are unique to each age-class the best strategy for conservation would be to retain all ages. Disturbed habitats are often considered to be more vulnerable to influxes of pest species. What if the higher species richness in one habitat is due to these invasive and/or non-endemic species? Species density patterns have been found to not always adequately reflect the fundamental difference in species composition of saproxylic organisms from different wood habitats (Jonsell and Weslien 2003; Similä *et al.* 2003; Sippola and Renvall 1999). The production of separate rarefaction curves for different components of the biota such as facultative and obligate species or red-listed and non-red listed species (Heilmann-Clausen and Christensen 2004) provides some information about the species associated with each habitat. However, the complete picture can only be seen with comparison of species composition. Species composition studies can be taken even further by considering the ecosystem

function of each species (Bengtsson *et al.* 2000). For example, does one habitat have key species crucial to the ecological functioning of that habitat?

While the ecosystem function for many species is difficult to assess due to lack of information, it is reasonable to compare different habitats by species composition for many organisms. Even if the species cannot be identified to a described species, the species can be classed as 'morphospecies' (Oliver and Beattie 1996b) to allow comparison between habitats. Advances in molecular techniques make it possible to compare the species composition across habitats using cryptic species such as fungi.

Species composition comparison between habitats is also vulnerable to differences in sampling effort. A difference in composition between two habitats may just be due to more species been collected from the habitat that has been more exhaustively sampled. One way to overcome this is to make a species composition comparison with datasets that have been standardised for sampling effort. The random sampling technique outline in this chapter produces a standardised species list with abundances that would be appropriate. A large amount of information is lost when reducing data to the smallest sampling effort, so it is recommended that both the reduced dataset and complete dataset be used to compare species composition. If both datasets are shown to have a different composition it is possible to conclude a difference between habitats. If a difference in species composition is only found in the complete dataset, then cautious interpretation is necessary that recognises the limitation on the result due to uneven sampling effort. This approach is used in the next chapter (Chapter 5) to compare the saproxylic beetle assemblages associated with different tree fractions and tree age-classes.

Summary

Species richness data need to be standardised for sampling effort before different sample sets are compared. Many techniques and metrics can be used for standardisation. One of the best techniques is rarefaction, but several methods of rarefaction exist. The new Mao-Tau sample-based rarefaction is not vulnerable to the two assumptions that are made in the calculation of classical and Coleman rarefaction, making it the preferred technique. Extrapolation techniques can be used to compare species richness at the more intuitive whole tree scale. A more complete

depiction of diversity should incorporate both the relative abundance of species and species assemblage composition. These measures are also vulnerable to differences in sampling effort. This may be overcome by using rank abundance curves and interpolated species lists, or assemblage composition comparisons.

The findings from this investigation of techniques to standardise sampling effort are used in the next chapter to compare saproxylic beetle assemblages found within living *E. obliqua* trees of different ages, and to investigate their association with different tree fractions. The most appropriate technique and measure to standardise species richness for this dataset was found to be Mao-Tau rarefaction based on surface-area. The best approach for comparing species assemblage composition is to contrast the findings from both a standardised dataset (i.e. the standardised species list with abundances produced by the random sampling technique outline in this chapter) and the original complete dataset.

Chapter 5

Saproxylic beetle diversity: Influence of tree age and wood fraction

5.1 INTRODUCTION

Larger-diameter, over-mature, moribund, veteran or old growth trees are a diverse structural and functional component of the forest landscape (Franklin *et al.* 2002). Their importance as a habitat for many species of arboreal, hollow-dwelling birds (Abbott 1998; Hanula *et al.* 2000; Virkkala *et al.* 1994) and mammals (Gibbons *et al.* 2002; Lindenmayer *et al.* 1991a; Mackowski 1987), and cryptic species such as wood decay fungi and bryophytes (Anderson 2001; Heilmann-Clausen and Christensen 2003; Nordén and Paltto 2001) is well documented. Many saproxylic beetle species are also known to be dependent on the habitat provided by old large trees (Alexander 2002; Grove 2001, 2002b; Grove 2002c; Ranius and Jansson 2000; Speight 1989). Forest practices can lead to a more uniform landscape in which old trees disappear or become more localised throughout the managed forest (Similä *et al.* 2002).

As a tree ages it develops an array of microhabitats including hollows, decayed wood, fissured bark and larger diameter branches. This high degree of habitat heterogeneity in a single tree may allow many specialist saproxylic beetles species to coexist. In some forest types, older trees can also support more specialist species than other dead wood fractions such as large diameter logs or coarse woody debris (CWD) and snags as they are longer lived and continue to generate habitat (Speight 1989). For example, in Sweden, old trees are a key habitat for 33 % of the 739 known threatened forest invertebrates (Berg *et al.* 1994). Old trees are also important as they are the precursor to large diameter logs or coarse woody debris which have been shown to support a diverse and unique suite of saproxylic invertebrates and wood decay fungi (Bader *et al.* 1995; Kappes and Topp 2004; Kolström and Lumatjärvi 2000; Kruys *et al.* 1999; Yee 2005).

Saproxylic insects are particularly vulnerable to forestry management practices that alter both the composition and availability of mature timber habitat (large-diameter trees, CWD and stags) (Alexander 1984; Grove and Tucker 2000). They represent a

disproportionally large percentage of nationally rare and threatened species in Europe (Grove 2001; Shirt 1987), where previous land use and intense forest management practices have altered much of the forest structure. One of the major changes in these forests is the reduction of larger diameter trees to such a level that they are now considered scarce in many regions such as Fennoscandianavia (Linder 1998; Linder and Östlund 1998).

In Tasmania, the lowland wet eucalypt forests are predominantly harvested by clear-felling, followed by a regeneration burn and sow regime (CBS) with a projected rotation length of 80-90 years (Hickey *et al.* 2001; Whiteley 1999). Harvested areas are generally on the scale of 50-100 ha. Each successive rotation will contribute to the alteration and simplification of the forest structure which may result in large areas of forest consisting of even-aged younger trees (Lindenmayer and McCarthy 2002; Lindenmayer *et al.* 2000). As there is a shorter history of intensive native forest management in Australia, there is still time to reduce any potential ecological impacts, through better understanding of saproxylic biodiversity and the underlying ecological processes early in this process of landscape alteration.

This chapter investigates saproxylic beetle assemblages associated with different tree fractions such as the stem, bark and branches. It explores this relationship across three tree age-classes representing young (pre-harvest), medium-age (harvest age) and old (old growth), with particular consideration of the effect of increasing tree structural complexity on the composition of invertebrate communities.

5.2 METHODS

Data Collection

Beetle abundance data were collected by emergence trapping of various tree fractions (stem wood, stem bark, branches, dead tops and hollows) from eighteen *E. obliqua* trees (six trees from each of three age-classes: young trees (69 years old); medium age trees (105 years old); and old trees (> 150 years old). For full details of the study site and sampling methods see Chapter 2.

In summary, eighteen trees were randomly chosen and felled from along two transects. Wood billets were cut from each stem at three standard heights (11m – 12 m above ground level; immediately below the crown; and within the live crown). Single half-metre long billets were sampled from medium-aged and old trees and a one-metre long billet from the young trees. A longer billet was taken for the young trees to increase the sampled volume of these small diameter trees. The bark was separated from the stem and each fraction placed in a separate emergence trap made of fine mesh. One-metre sections of two branches were collected from each tree and placed in individual emergence traps. When present, additional trees features such as hollows and dead tops were also sampled by sectioning out the complete feature for hollows and taking a half-metre section for the dead tops. These wood sections were also placed in separate emergence traps. These features were only found in the oldest age-class (see Chapter 2 for further details). Beetle emergence was monitored for eighteen months. All collected beetles were mounted and identified to morphospecies.

Several environmental variables were recorded for each tree (see Chapter 2 for a complete list of variables recorded).

Data Analysis

The diversity of saproxylic beetle communities present in different wood fractions (stem wood, stem bark and branches) for each age-class is compared by species richness and assemblage composition. Venn diagrams showing the distribution of saproxylic beetle species in each tree age-class were produced by pooling together the datasets for stem wood, stem bark and branches that had been standardised for sampling effort (these standardised datasets were produced for comparing species composition across the age-classes and details of the standardisation procedure are described below). Separate Venn diagrams were produced for all species, for facultative species and for obligate species.

Comparing species density

Species density for each age-class was evaluated by comparison of Mao-Tau rarefaction curves (Colwell *et al.* 2004) based on sampled surface area (stem wood

and branch sections) and weight (stem bark) calculated using *EstimateS* Version 7.5 (Colwell 2005). Sampled surface area for each wood section was pooled for each tree and the mean value calculated for each age-class. The cumulative surface area was then plotted against the number of species calculated by *EstimateS* Version 7.5 (Colwell 2005). This standardisation technique (Mao-Tau rarefaction) and metric (surface area) were chosen as the most appropriate for this dataset as detailed in Chapter 4.

For the comparison of species density between stem wood and branch sections, adjustment of the data was necessary to account for the fact that stem sections had the bark removed and the branches did not. This was done by amalgamating the datasets for the stem wood and stem bark sections to give a more complete dataset. This gave a reasonable approximation of the true species density, except for the oldest age-class in which not all the bark was retained and therefore the number of beetle species and individuals may be under-estimated. This has been taken into account in the interpretation of the results.

Species were divided into two groups, obligate or facultative saproxylic species, based on their dependence on dead wood. Mao-Tau rarefaction curves based on these two groups were produced to investigate if there was any pattern of preference for a tree age-class.

Comparing species richness by extrapolation to the volume of the whole tree

The mean number of expected species for each model per age-class was calculated as detailed in Chapter 4 and any significant difference in means tested using a one-way analysis of variance (ANOVA) using SAS 9.1 (Anon. 2002). For graphical comparison, extrapolated rarefaction curves for each age-class were calculated using the ECB model. Curves were extrapolated to the average number of species for each age-class at tree total volume, as it was not possible to extrapolate the rarefaction curves to total tree surface area, as not all the required measurements were taken during sampling (see Chapter 4 for further details).

Comparing species composition

The comparison of species composition is vulnerable to differing sampling effort. To minimise the effect of this, comparisons are made using the complete (original) dataset and a dataset that has been standardised for sampling effort (surface area sampled). The standardised dataset was calculated using the random sampling technique as detailed in Chapter 4. In summary, a reduction factor was calculated for each wood fraction (stem wood, branch or stem bark) to equate sampled surface area (stem wood and branch) or sampled weight (stem bark) to the smallest sampled surface area or weight. This factor was then used to calculate the expected number of individuals for each tree if the sampled amount was equal (i.e. *tree n* amount/smallest tree amount X *tree n* number of individuals). A species list for each wood fraction for each tree was determined by randomly selecting the calculated number of individuals from the corresponding complete dataset for each tree. For the comparison of species composition between the branch and stem (wood and bark) for all age-classes, the dataset was not standardised to the smallest sample size but to a cut-off value of $2m^2$ surface area sampled. All wood fractions with less than $2m^2$ surface area sampled were not included in the analysis.

Species composition for each wood fraction for all three age-classes was initially compared using Non-metric Multidimensional Scaling (NMS) and Multi-Response Permutation Procedures (MRPP) using the software package *PC-ORD* version 4 (McCune and Mefford 1999). Both these techniques are non-parametric multivariate statistical methods (see Chapter 2 for details). Data for NMS were $log_{10}(x + 1)$ transformed and vectors defined by beetle abundance with $r^2 > 0.2$ were overlaid. Untransformed data were used for MRPP analysis and calculated using the recommended Euclidean distance measure.

If no difference in species composition of wood fractions for the age-classes was found using unconstrained NMS ordination, then the data were also investigated using a constrained ordination technique, canonical analysis of principal coordinates (CAP), developed by Anderson and Willis (2003). This constrained ordination technique explores differences between *a priori* groups. CAP procedures were performed using a program by Anderson (2004) choosing the options of $log_{10}(x + 1)$ transformation, the Bray-Curtis distance measure and a test of significance using

9999 unrestricted random permutations of the data. The resulting canonical axes were plotted against each other using Microsoft Excel (Microsoft 1997).

Specialists of a tree age-class

Species preference for a tree age-class was investigated using two methods, Indicator Species Analysis (Dufrêne and Legendre 1997) and correlation analysis based on canonical axes derived from CAP (as detailed by Anderson and Willis (2003) (see Chapter 2 for further details). Indicator Species Analysis was conducted using the software package *PC-ORD* version 4. Significance was measured using Monte Carlo randomisation procedures using untransformed species data with IndVal $\geq$ 25, $p < 0.05$. Significant correlation was defined by $|r| > 0.3$ for each of the canonical axes obtained from the CAP output.

Comparing species composition and diameter

A canonical correlation analysis (CCoA) was performed using a program by Anderson (2004]) choosing the options of $\log_{10}(x + 1)$ transformation, the Bray-Curtis distance measure and a test of significance using 9999 unrestricted random permutations of the data to test if there is any relationship between species composition and diameter. The first matrix consisted of beetle abundance data per stem billet and per branch. The second comparison matrix consisted of the diameter data for each stem billet and each branch. Significant correlation is determined by eigenvalues (correlations) and the permutation test *p-value*.

5.3 RESULTS

Description of Fauna

In total 158 species of saproxylic beetles (4965 individuals) were collected as adults. The greatest number of species (data un-standardised by sampling effort) was collected from the stem wood (99 species, 1775 individuals and 32 unique species), then the branches (91 species, 671 individuals and 27 unique species) and stem bark (76 species, 1061 individuals and 18 unique species).

a) All species
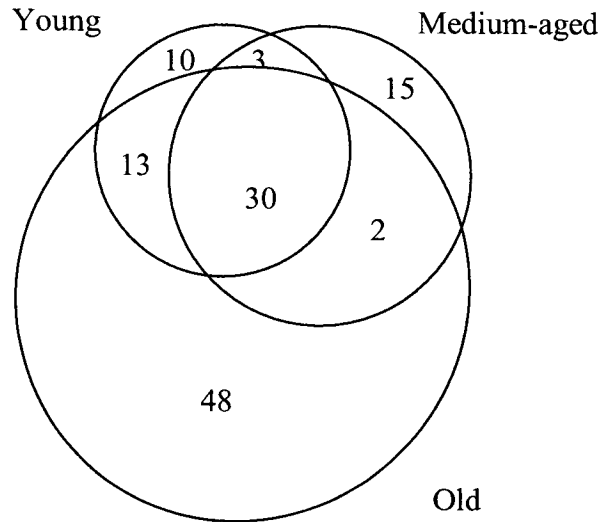
b) Facultative species
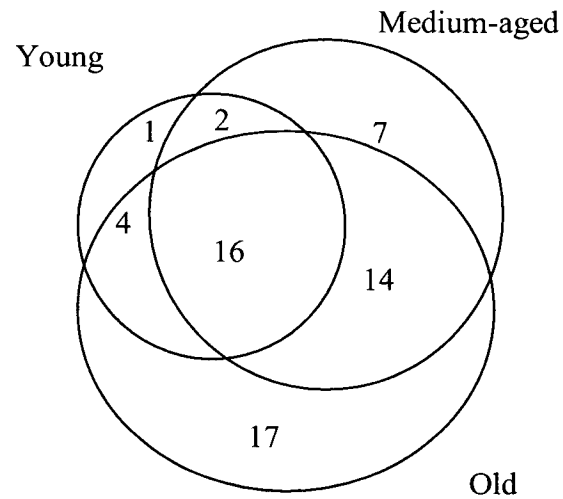
c) Obligate species
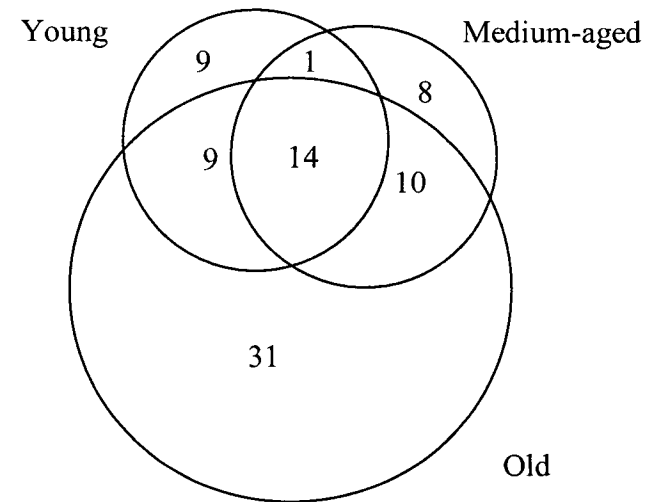
Figure 5.1 Venn diagram showing distribution of saproxylic beetle species in each tree age-class (pooled totals from stem wood, stem bark and branches which had been standardised by sampling effort) for (a) all species, (b) facultative species and (c) obligate species.

Comparison of species richness-Importance of tree age

◇ Young
■ Medium-aged
▲ Old
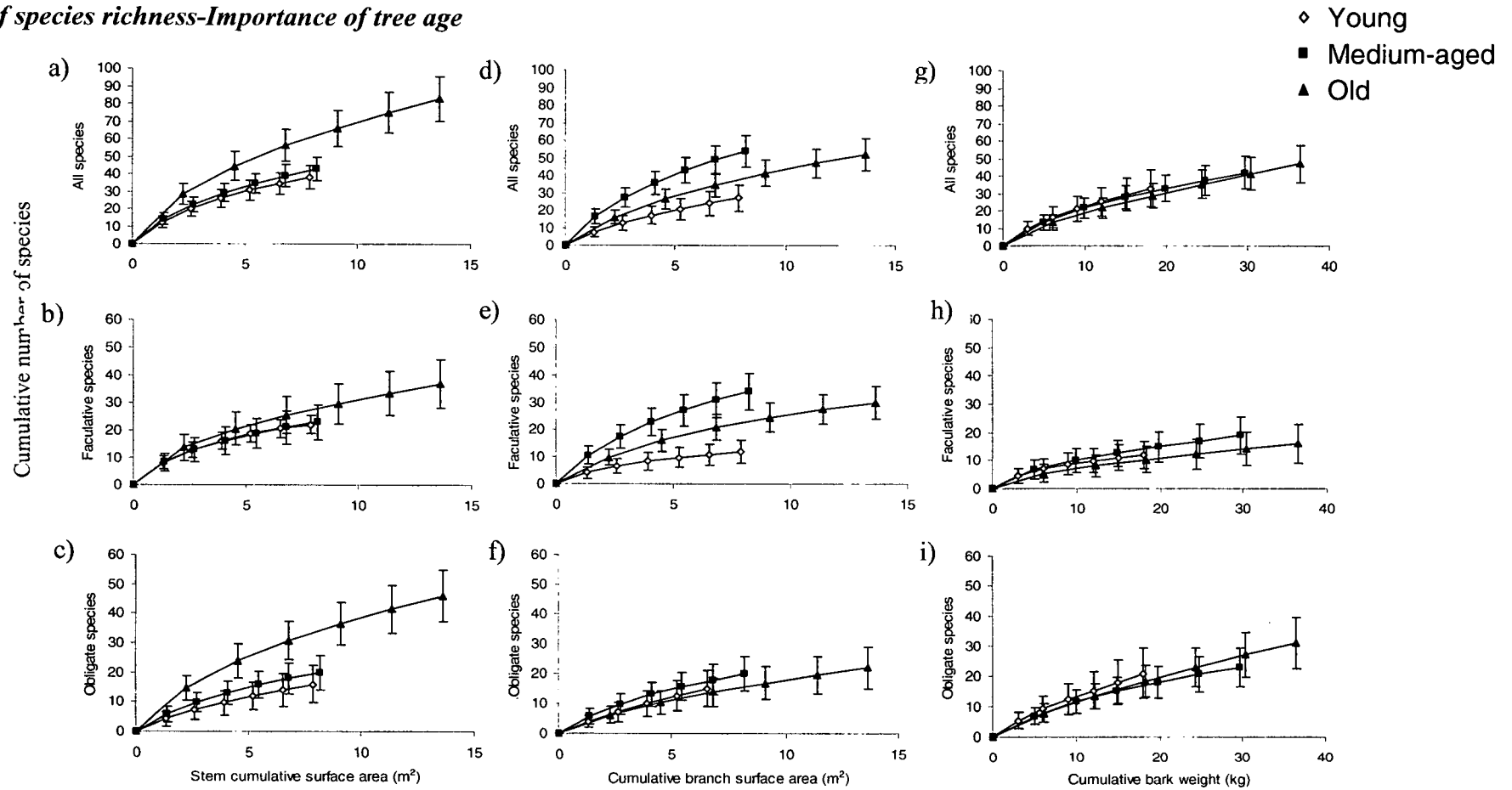
Figure 5.2 Mao-Tau rarefaction curves based on surface area of stem sampled (a-c), surface area of branch sampled (d-f) and amount of bark sampled (g-h) for all species (a,d,g), facultative species (b,e,f) and obligate species (c,f,i). Note the axes are different scales.

Saproxylic beetles were also collected from stem hollows from three old trees (34 species, 83 individuals and 8 unique species) and dead-tops from four old trees (38 species, 73 individuals and 7 unique species). The oldest tree age-class had a greater number of unique species than the two younger tree age-classes (Figure 5.1). This was most pronounced for the obligate species where the oldest trees had twice as many unique species as the number shared between all three tree age-classes.

The comparison of species density curves for stem wood sections show the oldest age-class to have a significantly higher species density than the younger two classes for all species pooled and for obligate species (Figures 5.2 a and c). All tree age-classes have a similar species density of facultative species (Figure 5.2b).

The oldest two age-classes have a higher species density of all species pooled, and of facultative species in branches, than the youngest age-class (Figures 5.2 d and e). This difference is significant for facultative species (Figure 5.2 e) and for all species pooled between the medium age trees and the youngest trees (Figure 5.2 d). All age-classes had a similar species density per kilogram of stem bark sampled (Figures 5.2 g, h and i).

Comparison of species density- Importance of different tree fractions

a)

b)

c)
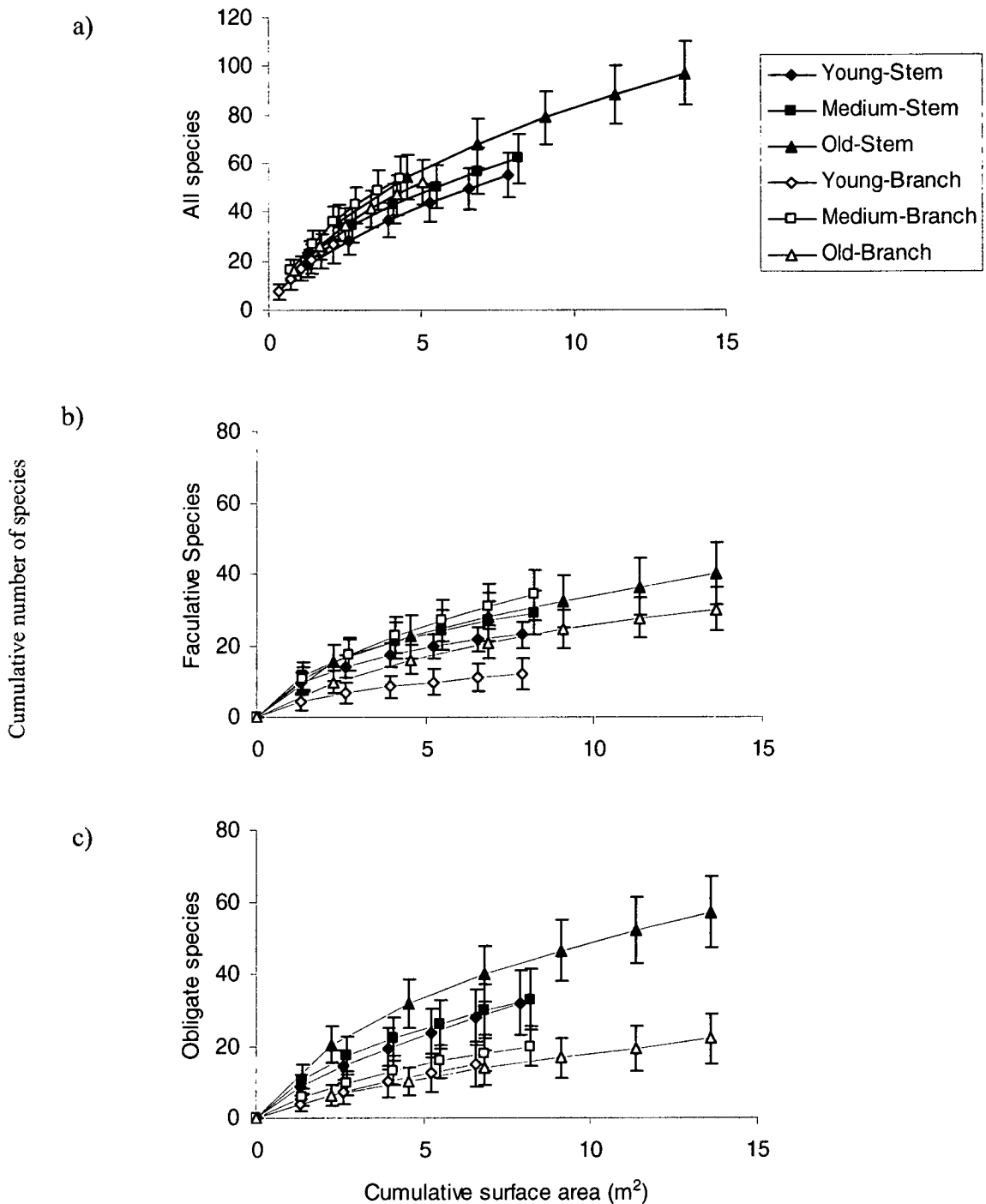
Figure 5.3 Mao-Tau rarefaction curves based on surface area of stem wood and branch sampled for all species (a), facultative species (b) and obligate species (c). Note the axes are different scales.

Species density for different wood fractions for all species pooled is similar (Figure 5.3 a). This pattern is slightly different for facultative species where the youngest branches have a significantly lower species density than all other age-classes or

wood fractions. When comparing obligate species density curves all stem wood fractions had a greater density than branch fractions. This was only significant for the oldest age-class. It is important to note that while this comparison has been done as a guide, the true number of species is underestimated for the stem sections of the older trees, as not all the bark was retained for sampling.

Comparison of species richness by extrapolation to the volume of the whole tree

Table 5.1 Mean extrapolated species richness based on saproxylic beetles emerging from stem wood sections for each age-class using four different models to estimate total species richness per tree. Standard error is shown. Letters a and b represent significant difference in means from ANOVA (p < 0.001) for each age-class per model.

Age-class	Raw Data from Stem Wood Samples	Exponential model	Clench model	ECB estimator	Logarithmic model
Young	12.3 ± 1.0^{b}	15.9 ± 1.7^{b}	22.3 ± 2.4^{b}	21.3 ± 1.2^{b}	32.0 ± 2.7^{b}
Medium	14.2 ± 1.6^{b}	16.8 ± 1.9^{b}	24.3 ± 2.8^{b}	25.6 ± 2.4^{b}	40.5 ± 5.1^{b}
Old	28.3 ± 3.4^{a}	32.6 ± 3.5^{a}	45.0 ± 5.0^{a}	45.3 ± 5.1^{a}	73.2 ± 8.8^{a}

All models calculated different values of expected species richness for each tree and mean expected richness for each age-class (Table 5.1). When the mean values of expected species richness for each age-class are compared, the results are consistent, irrespective of which of the four models is used (Table 5.1). The oldest age-class always had significantly higher species richness than the younger two age-classes. The two younger age-classes do not have significantly different means, but always follow the same pattern with the medium age-class having the higher species richness value.

Comparison of species composition

Stem Wood-Complete dataset

Aleocharinae TFIC sp 10
Aridius nodifer
Aridius costatus
Augenotus quadriguttatus
Clambus bornemisszai
Dohrnia miranda
Euplectops CHANDLER 'Tasmania 1'
Prionocyphon? TFIC sp 01
Prostomis atkinsoni
Pseudomicrocara TFIC sp 02
Tyrtaeosus ustulatus

a)

b)
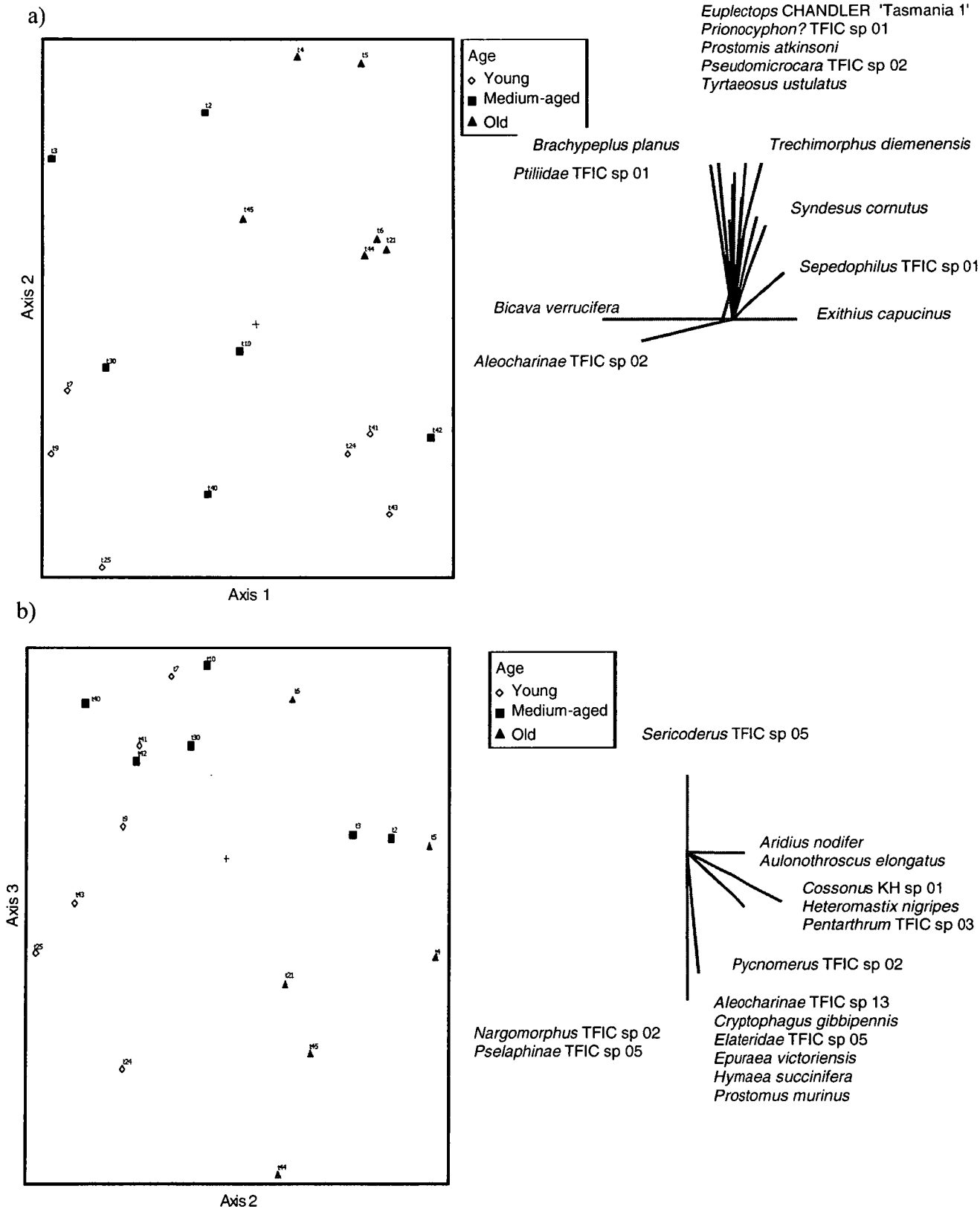
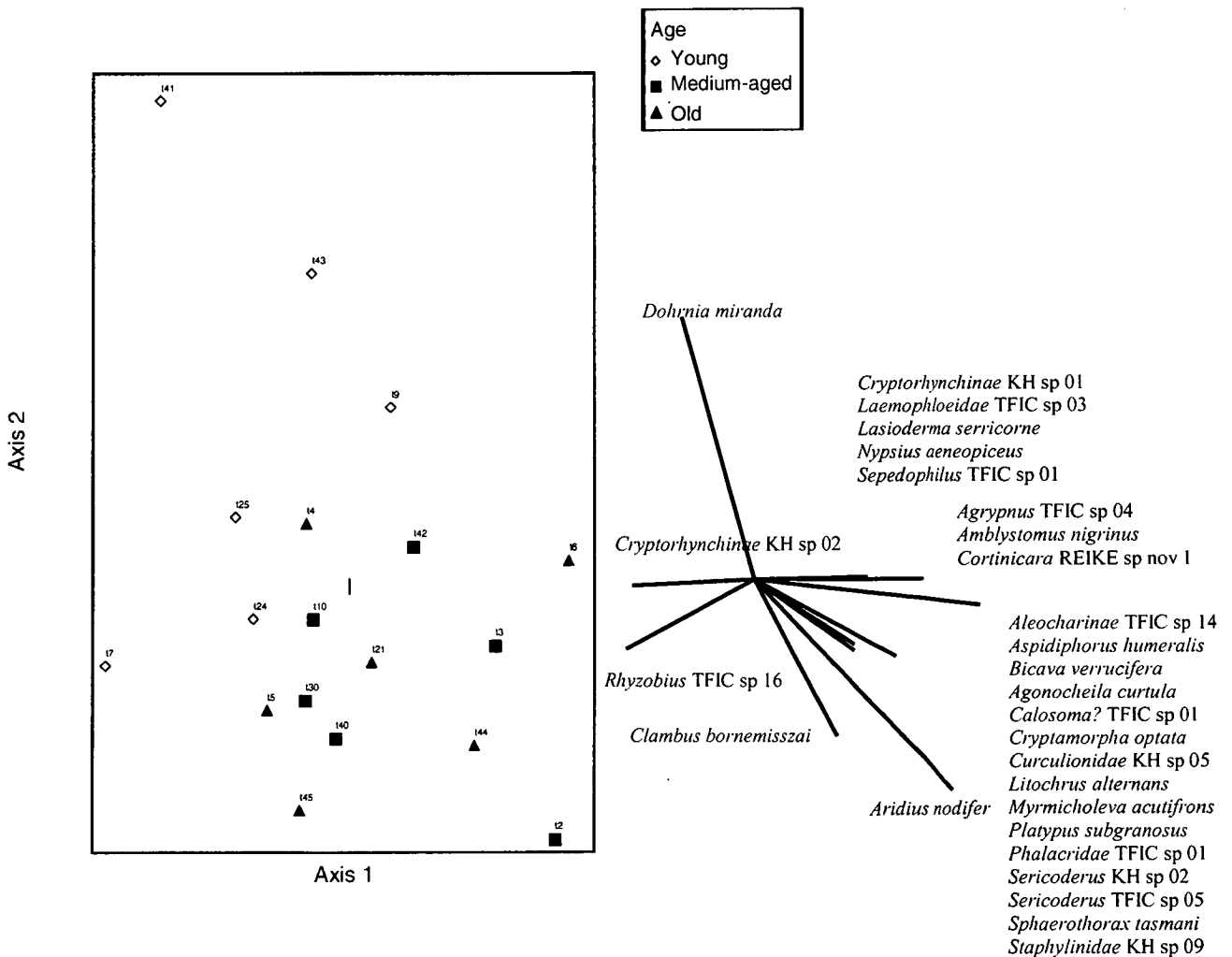*Figure 5.4 NMS ordination of saproxylic beetles captured by emergence trapping of stem billets for each tree age-class showing axes 1 and 2 (a) and axes 2 and 3 (b) from a total of three axes. Vectors ($r^2 > 0.2$) are defined by beetle abundance data; for greater clarity these are shown adjacent to the ordination. Abundance data were $log_{10}(x+1)$ transformed. Stress = 10.16*

The NMS ordination of the complete dataset shows a near-complete separation of the beetle assemblages along Axis 2 for the oldest age trees and the youngest age trees (Figure 5.4 a and b). This is supported by the MRPP result with a significant difference between the beetle assemblages from oldest and youngest trees (Table 5.2). The difference between the medium age-class and the youngest and oldest is not distinct, with some overlap in the ordination space (Figure 5.4 a and b).

Table 5.2 MRPP p-value results testing a null hypothesis of no difference in saproxylic beetle composition collected from the stems (wood) of each tree age-class for both the complete dataset and dataset standardised by surface area sampled.

Comparison Age-classes	All Species	Faculative Species	Obligate Species
Complete Dataset			
Young vs Medium	0.342	0.091	0.426
Medium vs Old	0.131	0.362	0.045*
Young vs Old	0.0008*	0.014*	0.082
Standardised Dataset			
Young vs Medium	0.461	0.100	0.519
Medium vs Old	0.453	0.543	0.011*
Young vs Old	0.038*	0.038*	0.050*

*Significant differences are marked with a *.*

The NMS ordination of the dataset standardised by surface area sampled shows the same pattern as the complete dataset with a near-complete separation of the beetle assemblages along Axis 2 for the oldest age trees and the youngest age trees (Figure 5.5 a and b). This is also supported by the MRPP result (Table 5.2). The difference between the medium age trees and the oldest trees is not distinct, with some overlap in the ordination space (Figure 5.5 a and b). The oldest age-class supported a different assemblage of obligate saproxylic beetle species compared to the other two age-classes (Table 5.2)

Stem Wood- Dataset standardised by surface area

a)

b)
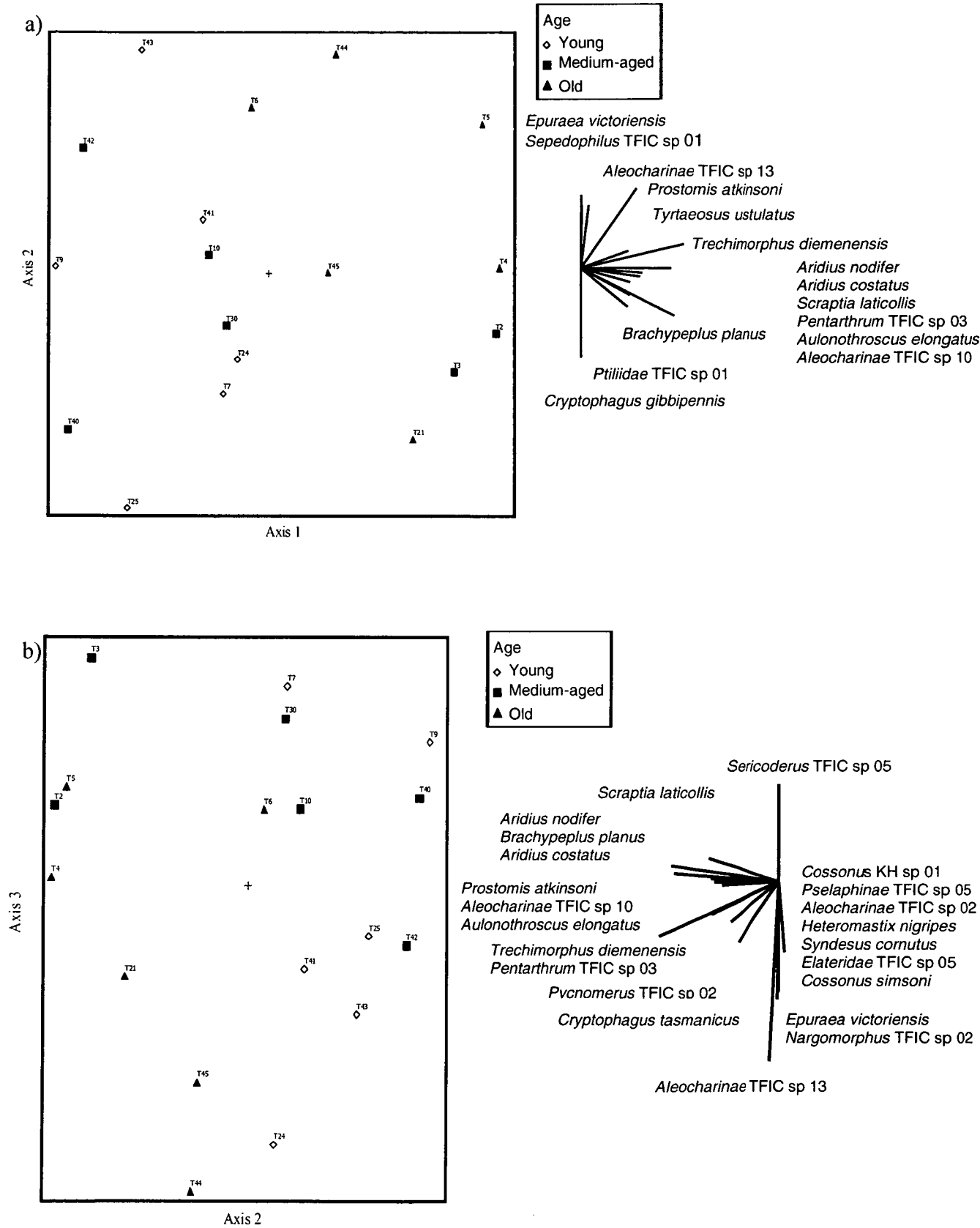
Figure 5.5 NMS ordination of the standardised dataset saproxylic beetles captured by emergence trapping of stem billets for each tree age-class showing axes 1 and 2 (a) and axes 2 and 3 (b) from a total of three axes. Vectors ($r^2 > 0.2$) are defined by beetle abundance data; for greater clarity these are shown adjacent to the ordination. Abundance data were $log_{10}(x+1)$ transformed. Stress=11.38

Stem Wood-Specialists of a tree age-class

The Indicator Species Analysis and correlation analysis using CAP found species with preferences for all age-classes, with many more species indicative of the oldest age-class (Table 5.3, Figure 5.6). A total of 43 species representing 23 different families from the complete dataset and 23 species from 12 families from the standardised dataset were found to be identifiers of the oldest tree age-class (Table 5.3). Four species (Curculionidae: *Pentarthrum* TFIC sp 03, Prostomidae: *Prostomis atkinsoni,* Staphylinindae: Aleocharinae TFIC sp 13 and Zopheridae: *Pycnomerus* TFIC sp 02) were highly significant for both the indicator species analysis and correlation analysis using the complete and standardised datasets. The complete dataset found three more species that were indicators of older trees for both types of analysis (Carabidae: *Trechimorphus diemenensis,* Curculionidae: *Cossonus* KH sp 01 and Lucanidae: *Syndesus cornutus).* Only one species was found to prefer the youngest age-class.
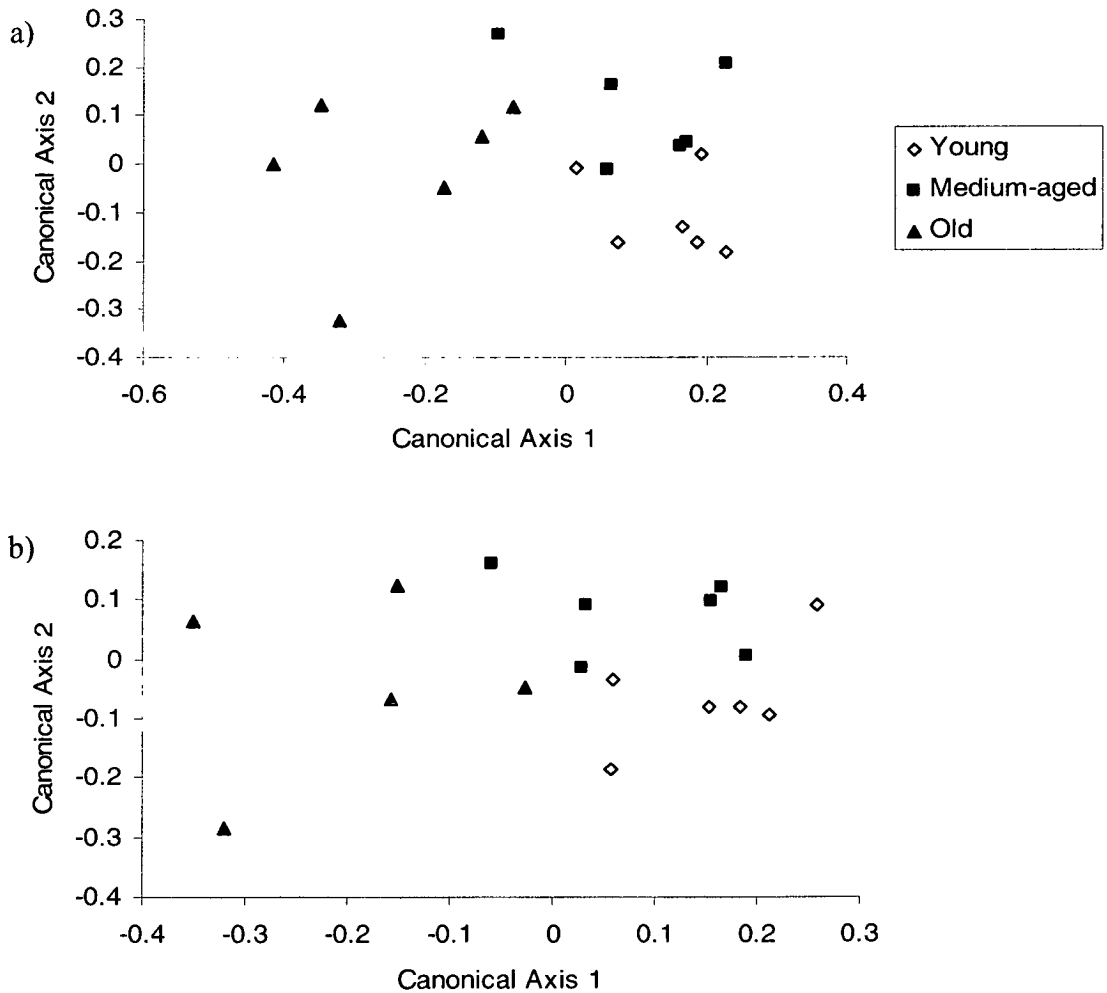
Figure 5.6 Scatterplots of the canonical axes 1 and 2 from the 2-dimensional solution of the constrained ordination of the a) complete dataset and b) dataset standardized by surface area for beetles collected from emergence trapping of stems for three age-classes. Data were $log_{10}(x+1)$ transformed.

Table 5.3 Combined results of correlation analysis based on canonical axis derived from CAP (Figure 5.6) and indicator species analysis for the effect of tree age-class.

Family	Species name	Complete Dataset			Standardised Dataset		
		Correlation coefficient with canonical axis	IndVal	*p*-value	Correlation coefficient with canonical axis	IndVal	*p*-value
Indicator species for the youngest age-class							
Staphylinidae	*Anabaxis* CHANDLER 'Type 1'	0.3670			0.4160		
Indicator species for the medium age-class							
Carabidae	*Trechimorphus diemenensis*					55.6	0.049
Corylophidae	*Sericoderus* TFIC sp 05	0.3413			0.3876		
Staphylinidae	Aleocharinae TFIC sp 14				0.3597		
Indicator species for the oldest age-class							
Aderidae	*Aderidae* KH sp 01	-0.4193			-0.4223		
Anobiidae	*Dryophilodes* KH sp 01	-0.4193					
	Anobiidae TFIC sp 09				-0.4223		
Cantharidae	*Heteromastix nigripes*	-0.3867			-0.3862		
Carabidae	*Trechimorphus diemenensis*	-0.4334	67.7	0.010	-0.7159		
Clambidae	*Clambus bornemisszai*	-0.4372					
Cleridae	*Lemidia subaenea*	-0.4193					
Cryptophagidae	*Cryptophagidae* KH sp 01	-0.5634			-0.4040		
	Cryptophagus tasmanicus	-0.5128			-0.3821		
Curculionidae	*Cossonus* KH sp 01	-0.3117	42.9	0.050			
	Cossonus simsoni	-0.3884			-0.3862		
	Curculionidae KH sp 02	-0.5018					
	Platypus subgranosus	-0.5018					
	Poropterus antiquus	-0.5018					
	Prostomus murinus	-0.3884					
	Exithius capucinus				-0.5187		
	Pentarthrum TFIC sp 03	-0.7320	64.9	0.010	-0.7225	66.7	0.016
	Tyrtaeosus ustulatus	-0.6231			-0.5160		
Elateridae	*Augenotus quadriguttatus*	-0.6458			-0.5166		
	Elateridae TFIC sp 05	-0.3884			-0.3862		
Latridiidae	*Aridius nodifer*	-0.5866			-0.4614		
	Aridius costatus	-0.4552					
	Cortinicara REIKE sp nov 1	-0.4074					
Leiodidae	*Nargiotes gordoni*	-0.3884					
Lucanidae	*Syndesus cornutus*	-0.7583	66.7	0.017	-0.3862		
Melandryidae	*Orchesia ?austrina*	-0.3884					
Nitidulidae	*Brachypeplus planus*	-0.4538					
Oedemeridae	*Dohrnia miranda*	-0.6152			-0.5187		
Phloeostichidae	*Hymaea succinifera*	-0.3192			-0.4164		
Prostomidae	*Prostomis atkinsoni*	-0.8127	66.7	0.017	-0.8454	66.7	0.018
Ptiliidae	*Ptiliidae* TFIC sp 01	-0.3182					
Scydmaeidae	*Scydmaeidae* TFIC sp 04	-0.5010					
Staphylinidae	Aleocharinae TFIC sp 03	-0.4193					
	Aleocharinae TFIC sp 07				-0.3522		
	Aleocharinae TFIC sp 10	-0.7039	55.6	0.039			
	Aleocharinae TFIC sp 13	-0.5946	80.7	0.010	-0.4895	63.5	0.021
	Euplectops CHANDLER 'Tasmania 1'	-0.4025					
	Falagria TFIC sp 04	-0.4193					
	Macrodicax TFIC sp 01	-0.5018					
	Sagola rugicornis	-0.3475					
	Sepedophilus TFIC sp 01	-0.3914			-0.4105		
	Staphylinidae KH sp 10	-0.5018					
	Staphylininae TFIC sp 03	-0.5018			-0.5187		
Tenebrionidae	*Diemenoma commoda*	-0.5018					
Throscidae	*Aulonothroscus elongatus*	-0.4145			-0.4464		
Zopheridae	*Pycnomerus* TFIC sp 02	-0.6957	80.6	0.002	-0.4809	61.1	0.026

Stem Bark- Complete dataset and dataset standardised by surface area

No useful NMS ordination and no significant difference was detected in the beetle composition of stem bark for the three age-classes for both the complete dataset (MRPP value $p = 0.555$) and the dataset standardised by surface area sampled (MRPP value $p = 0.498$). A constrained ordination (CAP analysis) on both datasets also found no significant difference for either the complete dataset (squared canonical correlation $\delta^2 = 0.609$, $p = 0.112$) or the dataset standardised by surface area sampled (squared canonical correlation $\delta^2 = 0.533, p = 0.124$).

Branch-Complete dataset and dataset standardised by surface area

Figure 5.7 NMS ordination of saproxylic beetles captured by emergence trapping of branches for each tree age-class showing axis 1 and axis 2 from a total of three axes. Abundance data were $\log_{10}(x+1)$ transformed. Vectors ($r^2>0.2$) are defined by beetle abundance data; for greater clarity these are shown adjacent to the ordination. Stress = 17.09541

The NMS ordination of the beetle assemblages collected from branches shows a clear separation between the youngest age-class and the two oldest age-classes (Figure 5.7). The MRPP results support this finding with a significant difference between the youngest and medium age trees ($p = 0.001$) and the youngest and oldest age trees ($p = 0.01$). No significant difference was found between the medium age and old trees ($p = 0.61$). Only one species was found to be significant for an age-class using indicator species analysis. *Ptiliidae* TFIC sp 01 (Ptiliidae) was significant for the medium-aged trees (*IndVal* $=58.8$, $p = 0.02$).

No useful NMS ordination was found for the standardised branch dataset. The CAP analysis of the dataset standardised by surface area found no difference between the beetle assemblages from each age-class (*squared canonical correlation* $\delta^2 =0.51$, $p = 0.465$).
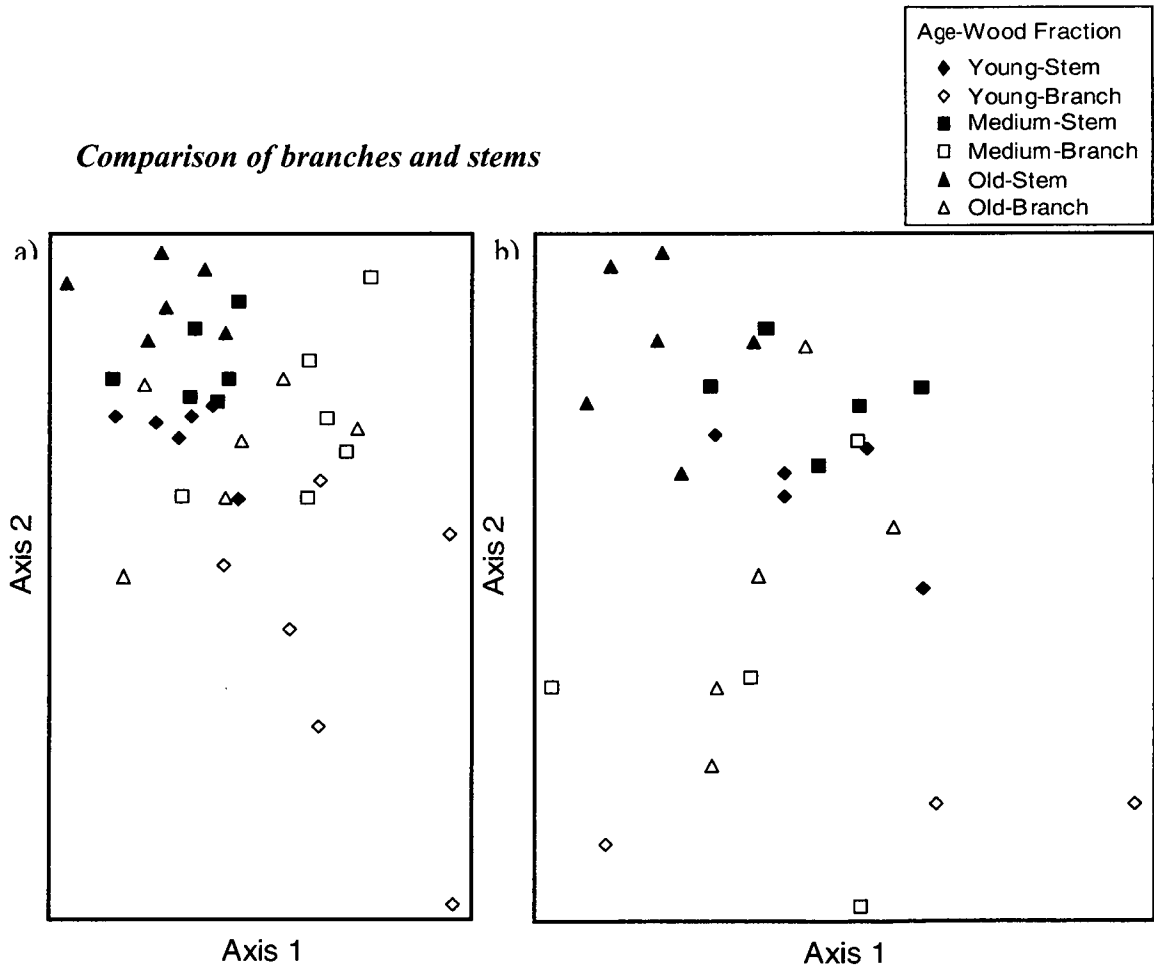
Figure 5.8 NMS ordination of the a) complete dataset and b) dataset standardised by surface area sampled of saproxylic beetles captured by emergence trapping of stems (wood and bark) and branches for each tree age-class showing axis 1 and axis 2 from a total of two axes. Abundance data were log$_{10}$(x+1) transformed. Stress a) 17.15 and b) 12.00.

The NMS ordination analysis of the complete dataset of saproxylic beetles from stems (pooled stem wood and stem bark) and branches for each age-class found a near-complete separation of the youngest branches from all other stems and branches (Figure 5.8a). This was supported by the MRPP result with a significant difference found for beetle assemblages from the youngest branches and all other stems and branches (Table 5.4 and Appendix 5.1). All other branches and stems from each age group were found to overlap with at least one other wood section. The NMS ordination of the dataset standardised by surface area sampled (to a cutoff value of a minimum surface area of 2 m^2) had no clear separation, with all branches and stems from each age group overlapping with at least one other wood section (Figure 5.8b). This was supported by the results of several MRPP analyses (Table 5.4 and Appendix 5.1).

Table 5.4 Summary of tree age-wood fractions that have a similar species composition according to MRPP analysis*.

Tree Age-Wood Fraction	Complete Dataset	Standardised Dataset
Young Branch	None	All branches; medium-aged stem
Young Stem	Old branch; medium-aged stem	Medium-aged and old branches
Medium-aged Branch	All branches; medium-aged stem	All branches; young and medium-aged stem
Medium-aged Stem	Medium-aged branch; all stems	All branches; old stem
Old Branch	Medium-aged branch; young stem	All branches; young stem
Old Stem	Medium-aged stem	Medium-aged stem

* Appendix 5.1 lists MRPP values for each pair-wise comparison.

Species composition and diameter of wood fraction

A CCoA analysis of the complete dataset of saproxylic beetles from stems and branches from each age-class and diameter found a strong positive correlation between beetle composition and diameter (eigenvalues (correlations) = 0.861, $p = 0.0001$). The same analysis using the dataset standardised by surface area sampled also found a strong correlation with diameter (eigenvalues (correlations) = 0.794, $p = 0.0001$).

5.4 DISCUSSION

Diversity in relation to tree age-class

This has been the first study to investigate saproxylic beetle assemblages in *Eucalyptus obliqua* trees and has found a high level of diversity in all age-classes, with the pattern of species richness or density and assemblage composition varying with tree age. The oldest trees hosted a greater number of species and a higher number of unique species than did the younger trees for both un-standardised datasets and for datasets standardised by surface area sampled. While old trees have been documented as the preferred substrate for many saproxylic species including the rarest and most threatened insects (Jonsell *et al.* 1998; Nilsson and Baranowski 1997; Ranius 2002; Warren and Key 1991), the majority of studies have focused on either standing dead trees (snags) (Hammond 1997; Hammond *et al.* 2001; Sverdrup-Thygeson and Ims 2002), stumps (Irmler *et al.* 1996; Jonsell *et al.* 2004; Lindhe and Lindelöw 2004) or dead wood on the forest floor (Irmler *et al.* 1996; Schiegg 2001; Wikars *et al.* 2005; Yee 2005), or have considered the age of the stand as a whole (Grove 2002b; Hammond *et al.* 2004; Martikainen *et al.* 1999; Martikainen *et al.* 2000; Siitonen *et al.* 2000), with few directly investigating the diversity associated with trees of different ages. Therefore, it is difficult to directly discuss the findings from this study in relation to previous studies. Older stands, which include trees, snags and downed wood of different ages and sizes, have been linked with a higher species richness and diversity (Hammond *et al.* 2004). A study in an Australian lowland tropical rainforest found that living tree basal area was the best predictor of saproxylic beetle species richness and assemblage composition, with positive correlation between tree basal area and saproxylic beetle diversity (Grove 2002b). Studies conducted on downed dead wood (Kappes and Topp 2004), snags (Hammond *et al.* 2001; Vaisanen *et al.* 1993) and stumps (Irmler *et al.* 1996) on various tree species and in various geographical locations have often indicated that older, larger diameter wood features are associated with higher diversity of saproxylic beetles than younger, smaller diameter wood features.

The findings from some of these studies have recently been questioned, as the general conclusion that older larger diameter wood is better for diversity may be an artefact of uneven sampling size (i.e. more was sampled in the larger diameter wood) and that it merely reflects the simple relationship between species richness

and amount of substrate. Several recent studies that have taken sample size into account have found smaller diameter wood to have either equal or greater species richness and density (Lindhe and Lindelöw 2004; Heilmann-Clausen and Christensen 2004; Schiegg 2001; Yee 2005). This study has attempted to standardise the data to minimise the effects of uneven sampling effort, but still finds that older, larger diameter trees have significantly higher species density than younger, smaller diameter trees.

This study has also investigated changes in assemblage composition, which is not as commonly incorporated into studies comparing diversity values of different aged stands or wood dimensions. This is an important feature of diversity to incorporate, as species density patterns have been found to not always adequately reflect the fundamental difference in assemblage composition of saproxylic organisms from different wood habitats (Jonsell and Weslien 2003; Similä *et al.* 2003; Sippola and Renvall 1999). Beetle assemblage compositional data are also vulnerable to uneven sample size. This study has attempted to standardise the assemblage composition data, but as a large amount of information is lost when reducing data to the smallest sampling effort, both the results for the standardised dataset and complete dataset have been presented to compare species composition. Overall, this study has found a difference in assemblage composition between the age-classes, particularly between the youngest and oldest trees. In a study on *E. obliqua* logs, Yee (2005) also found changes in assemblage composition between large and small diameter logs. While assemblage composition is not as commonly investigated, several other studies have focused on the occurrence of red-listed species. The results have been conflicting, perhaps reflecting the differing forests and their management histories. Some studies have found smaller diameter wood to host more threatened species than larger-diameter wood (Schiegg 2000a), while other studies have found that larger diameter wood is particularly important for red-listed species. For example, Lindhe (2004) investigated saproxylic beetles in cut high stumps in Sweden and found that red-listed fauna favoured the larger diameter (>0.6m) stumps over medium (>0.3m) stumps. The proportions of red-listed species were found to be correlated to the stump diameter.

While standardisation is a useful technique to accurately compare the diversity of samples of uneven size it can limit the analysis to replicated features, hence

omitting some components that may be linked with age, and hence only found in a particular age of tree. For example, in this study the older trees had two important additional features, stem hollows and dead tops of the stem, which were only found in these older trees. As this was an additional volume of wood only sampled from one age-class, the results from this have not been able to be standardised and have not been included in any of the analysis. Additional species that were not found in any other wood fraction were present in both of these features, increasing the overall species richness of the oldest trees. So while standardisation of sampling is important, as Hammond (2004) suggests, older larger diameter wood (trees, logs and snags) may need to be sampled more intensively than younger smaller diameter wood to ensure adequate sampling of the wider range of diverse habitats present.

Which tree fractions contribute most to the differences in diversity?

The investigation of different tree fractions found no difference in saproxylic beetle richness or assemblage composition in the stem bark fraction among the three tree age-classes. North American studies investigating invertebrate biodiversity and bark traits have found the bark on older trees to be associated with a higher diversity of invertebrates per unit area than younger trees (Hanula *et al.* 2000). This change in diversity with tree age has been linked to the increasing thickness and structural complexity of the bark in mature trees (Hanula *et al.* 2000; Nicolai 1986). Thus, it may have been expected that the older trees in this study would have a different fauna and greater species richness than the younger trees. However, these studies used different trapping methods (intercept and drift nets) which captures a large proportion of the transient fauna landing on or travelling along the trunk, compared to the emergence trapping method used in this study which mainly captures those invertebrates living within the bark. Also these studies have analysed all invertebrates captured on the bark, not just the saproxylic beetles, as in this study, which may explain the variation in findings between the studies. Other factors that may have caused the findings to vary are the different tree species investigated, and the tree age and bark thickness variation between the trees investigated. In the Hanula *et al.* (2000) study, the trees ranged from 20-95 years old and the bark thickness varied from 1-2.5cm. Hence, included trees of a much younger age than the current study, which may have bark with different properties.

In the current study only a small difference was noted in bark thickness with tree age (0.6-1cm, *personal observation*), which may also account for no difference being noted among the age-classes. While the relationship between bark thickness and invertebrate diversity has not been directly studied in eucalypts, a study conducted by Majer (2003) in Western Australia investigating invertebrate richness and different eucalypt species did find that different tree species that had bark with the same thickness had similar species richness.

Saproxylic beetle species richness and assemblage composition of branches was found to vary by age-class. In particular, fewer beetle species (notably facultative saproxylic beetle species) and a different beetle fauna were associated with the branches from the youngest trees compared to the two older age-classes. This difference in fauna was not found when using the standardised dataset. This may have been due to too much information being lost during the standardisation procedure, in which the larger branches (from the older trees) were standardised to the surface area sampled from the smallest branch and reducing the data to fewer than twenty individuals per tree. In circumstances such as this when standardisation reduces the comparable data to such a degree, the validity of standardisation is questionable.

One possibility for the lower beetle species richness, particularly for the facultative saproxylic species, of the branches of the youngest trees is the composition of the bark present. The branches on the youngest trees were relatively newly developed, with a small diameter and in most cases still possessing 'juvenile' or 'small twig' bark (Jacobs 1955). This type of bark has a thin corky or phellem layer with little build-up of dead outer bark. This is quite different from the 'mature' bark found on older *E. obliqua*, which is a stringybark eucalypt. This type of eucalypt retains the outer rhytidome and develops a thick dead outer bark layer (Jacobs 1955). All the branches from the medium age and oldest trees possessed this 'mature' bark. Facultative beetle species are often those associated with the surface of the wood (subcortical and bark), and the thicker mature bark of the medium age and older trees is likely to provide both a larger quantity and a more suitable habitat for many species than the thin 'juvenile' bark of the branches from the youngest trees. This may also explain why the younger trees had a different assemblage composition of saproxylic beetles compared to both the medium-aged and old trees for the

unstandardised dataset. The overlay of the beetle species associated with the different age-classes shows the main species driving the separation between the youngest age-class and the two old age-classes are facultative saproxylic species. This is also supported by the Indicator Species Analysis, although only one species was found to be faithful to a particular age-class.

Another explanation for the change in diversity with age may be attributed to the diameter of the branches studied for the different age-classes. The branches sampled on youngest trees were ranging from 3.5-7.5 cm in diameter with a mean diameter of 5.2 ± 0.5 cm (for more details see chapter 2), while the medium and oldest trees had branch diameters ranged from 4-12 cm with a mean diameter of 7.1 ± 0.9 cm and 4-24 cm with a mean diameter of 11.5 ± 2.1 cm respectively. The sampled branches were representative of the range of branch diameters present on the trees from each age-class. The larger diameter branches have a larger volume of heartwood, which may provide a more stable microclimate and a more diverse habitat for colonisation. A more detailed discussion of these factors can be found in later in this discussion in relation to diversity changes in the stem. If the availability of heartwood is a significant factor in determining the species composition between the tree age-classes in this study, it would be expected that more wood-dwelling species would be found in the older, larger diameter branches found on the older trees. As no wood-dwelling species were found to be indicators of the two oldest age-classes and only one wood-dwelling species (Curculionidae: *Platypus subgranosus*) was found to be correlated in the ordination, it can be suggested that the volume of heartwood in a branch is not as important as the type of bark present on the branch, as a factor influencing both species richness and assemblage composition.

The most pronounced variation in saproxylic beetle diversity between the different aged trees was found in the stem wood fraction. The stem of the oldest trees supported a significantly greater number of saproxylic beetle species than the younger two age-classes, for un-standardised data, data standardised by surface area and when extrapolating the data to the total size of the tree. Saproxylic beetle composition differences also existed, particularly between the youngest and oldest trees.

A closer examination of the results helps to understand what is driving the diversity difference among the stems of different age-classes. When the saproxylic beetle assemblage is divided into facultative and obligate saproxylic species, it is the species richness and assemblage composition of the obligate saproxylic species that explains the majority of the variation between the age-classes, particularly the difference between the medium-aged and oldest trees. Facultative species richness does not vary between the age-classes and the assemblage composition of facultative beetle species varies only between the youngest and oldest age trees.

This strong variation in the diversity of obligate saproxylic species may be explained by the increase in dead wood or suitable habitat (wood decay) within the stem of the older trees. Old trees are generally associated with more wood decay (Boddy 2001; Rayner and Boddy 1988) and significantly more decay was found in the stems of older trees than the two other age-classes (see Chapter 6). Coupled with an overall increase in the amount of decay is an increase in the diversity of habitat types for saproxylic beetles. The formation of habitat (such as decayed wood and wood altered by insect attack) follows many successional pathways depending on the sequence of species involved and other environmental factors, which results in numerous individual microhabitats within the stem (Martikainen *et al.* 2000; Nilsson *et al.* 2002; Speight 1989). The older a tree, the greater the probability it has been exposed to more stochastic events that cause damage (Adkins 2006), and which provide entry points for wood decay fungi, saproxylic beetles and other invertebrates. Over time, each damage event will be associated with a different set of environmental conditions which creates an opportunity for different species of fungi and invertebrates to colonise the wood (Heilmann-Clausen and Christensen 2004). The action of different species can alter the physical and chemical properties of the wood in different ways, increasing the diversity of habitat within the stem. Some fungi and faunal communities appear to be restricted to large or old trees (Parsons *et al.* 2003; Ranius and Jansson 2000), and this may be due to a dependence on specific successional pathways, which are required to provide a habitat suitable for specialised successor species (Komonen 2003; Niemelä *et al.* 1995; Renvall 1995). Large old trees, as well as having a longer and potentially more diverse colonisation history, have a greater surface area available for individual colonisation or infection. This allows for more new entry points for

different species of wood-inhabiting organisms than a younger, smaller tree (Heilmann-Clausen and Christensen 2004).

The finding that the stems of old trees are associated with significantly more obligate species, and have a different assemblage of obligate saproxylic beetle species, indicates the importance of old trees, as they not only support a greater number of species but they also support more species which are entirely dependent on dead wood for their continued existence. A review of habitat associations of saproxylic beetles in Sweden found that the majority of red-listed species (434/542, 80%) live in the main trunk of the tree, with most species preferring the larger diameter wood (Jonsell *et al.* 1998). While there is little information regarding the specific habitat requirements of the obligate beetle species captured in this study, some species have been associated with habitats that are unique to older trees (see Chapter 6). From studies in Northern and Western Europe it is known that certain old trees with heart rot decay have a high conservation value for saproxylic beetle diversity (Dudley and Vallauri 2004; Key and Ball 1993; Nilsson *et al.* 2002; Ranius 2002; Vallauri *et al.* 2002). Particular species are known to be unique to certain habitats found only in older trees, for instance the scarabaeid *Osmoderma eremita* which lives only in hollows in deciduous trees (Ranius and Nilsson 1997). Also, a review of beetle habitat associates in Sweden found that 64 out of 107 species living in hollow tree trunks were specialists (Jonsell *et al.* 1998). Two species that this study found to be indicators for old stems, *Prostomis atkinsoni* (Prostomidae) and *Pycnomerus* TFIC sp 02 (Zopheridae) were also found to be associated with old or large *E. obliqua* logs of an intermediate decay stage in Tasmania's wet forests (Yee 2005). In logs, both beetle species were associated with a specific habitat type, a brown rot that occurred in the inner heartwood. This rot type preferentially occurred in large diameter logs. A similar association between this inner brown rot and older larger diameter trees and between the brown rot and beetles was found in this study in the living tree (see Chapter 6). This highlights the potential reliance of a beetle species on the habitat provided by an old tree, and its subsequent large diameter log. It also highlights that old eucalypt trees in Tasmania may be as important for saproxylic beetle biodiversity as certain old trees in Europe.

European and North American beetle species in the same genus as the four main indicator species of older trees in this study (*Prostomis atkinsoni* (Prostomidae), *Pycnomerus* TFIC sp 02 (Zopheridae), *Pentarthrum* TFIC sp 03 (Curculionidae),

Aleocharinae TFIC sp 13 (Staphylinindae)) have had drastic declines in population and range, with some regional extinctions occurring. For example, *Prostomis mandibularis*, which is associated with red-brown muddy rot in oak logs (Yee 2005), is extinct in the United Kingdom (Alexander 2002; Boswijk and Whitehouse 2002). *Pycnomerus terebrans*, which is associated with red rotten wood of old hardwood trees, is also extinct in Britain (Buckland and Dinnin 1993), and close to extinction in parts of Germany (Wenzel 2002). Several species in the staphylinid subfamily Aleocharinae, that are associated with older trees, are known to be nationally scarce or listed in the red data book of vulnerable and threatened species for Britain and Ireland (Alexander 2002). Two species *Pentarthrum blackburni* and *Pentarthrum obscura* are listed as possible candidates for the American Environmental Protection Agency's (EPA) register of Endangered and Threatened Wildlife and Plants. Yee (2005) suggests that both *Pycnomerus* TFIC sp 02 and *Prostomis atkinsoni* are likely to be vulnerable to a reduction in the availability of large trees or logs and to habitat fragmentation due to their likely low power of dispersal and specificity to habitat types found in larger diameter wood.

The younger trees had few indicator species and few unique species, which is the same trend that has been found for both logs and snags. Yee (2005) found many species to be associated with large diameter logs but only two species were found to be indicators of small logs. A study of *Populus spp.* snags of different diameters in boreal forest in Canada found similar trends (Hammond *et al.* 2001). This emphasises that while younger trees are also important for saproxylic beetle diversity it is the oldest trees that support a suite of species that cannot be found in younger trees. This concept is very important as it is the older trees that are more vulnerable in the production landscape where they are removed during forest harvesting and not replaced under the current prescribed rotation length. The impact of this on saproxylic beetle diversity will depend on many factors, including a species' ability to overcome spatial and temporal loss of habitat. This is influenced by a species' geographical distribution, dispersal ability and how specific its habitat requirements are. This is discussed further in Chapter 8.

The total species richnesses of branches and stems from all age-classes were found to be similar. When taking into account this result it is important to consider that due to sampling issues, the total species richness for the older stems is under-estimated (see methods for further details). However it has been included as it is in contrast to some other studies comparing the diversity of branches and stems. Also, when only the obligate species are considered the older trees have significantly more species (even when the true species richness is under-estimated). A study conducted by Schiegg (2001) investigating saproxylic beetles on downed stems and branches of beech in Central Europe found limbs (branches) hosted more species and had a higher diversity than trunks (stems). This was true for both un-standardised and standardised data. Another study by Hilt and Ammer (1994) found contrasting results for different tree species, with the dead wood of smaller dimensions from spruce hosting more exclusive species but with an opposite result for oaks. Thus, it appears as if the significance of wood dimension for saproxylic insects varies among tree species, which may explain why no difference in total species richness was found in this study.

Schiegg (2001) studied branches and stems in a medium stage of decay, in which the wood is partly softened and there are clear signs of colonisation by saproxylic insects and fungi. As the stage of decay influences the assemblage composition of saproxylic beetles, this may be another reason why the downed branches had greater species richness than stems, but no difference was found for the present study. Schiegg (2001) proposed that one of the reasons for the higher species richness in branches is that the rotting process and colonisation of insects usually starts before they break off; therefore branches may contain species from the canopy. The majority of the branches in this study did not have any rot present, with only 6 out of a total 66 branches showing any decay.

In the present study all stems supported more obligate saproxylic species than branches but this was only significant for the oldest trees. The ordination shows that the clearest difference in beetle aseemblage composition occurs in the branches from the youngest trees and the oldest stems, while the branches of the medium-age and oldest trees and the stems of the youngest and medium-aged trees have a similar species composition. This should be interpreted cautiously as these data have not been standardised as too much information was lost when standardising to the

amount of wood sampled from the smallest branch. The suggested reasons for this finding are generally the same as those suggested for why the stem wood of the smaller diameter younger trees had fewer obligate species than the stem wood of older trees. Older (larger diameter) wood has a more stable microclimate (Boddy 1983; Kolström and Lumatjärvi 2000), more heartwood to colonise, and more habitat (wood in different degrees of decay) for the obligate saproxylic beetles.

Is diameter important?

Many of the identified factors differentiating tree age-classes based on species richness and composition indicate that the dimensions of the wood fraction are important. Wood size (for both branches and stems) is inherently linked to tree age. Although anomalies and a large variation in actual size occur within a certain age, the general pattern is the older the wood, the larger the diameter. A strong positive correlation was found between wood diameter and species composition for both branches and stems. So diameter may be partially a surrogate for age, but there may be additional aspects that are related to diameter (e.g. a larger diameter wood fraction may be more buffered and provide a more stable microclimate). Also, the CCoA analysis tests only for a relationship between the measured variables and species composition. Other factors (such as sun-exposure and the presence and absence of certain fungi) may also be correlated to species composition and may explain some of the variation not explained by diameter. Further studies would be needed to elucidate these factors.

It has been suggested that branches in the crown of a tree are analogous to trees in a forest (Ishii and McDowell 2001; Bar-Ness 2005), with the range of sizes (and ages) of branches in a crown corresponding to the range of sizes (and ages) of trees within a forest. Results from this current study support this concept, with similar saproxylic beetle assemblage composition between some branches and stems (e.g. medium-aged and older branches have a similar beetle assemblage composition to the stems of younger trees). This highlights the value of the structural complexity found within an older tree, as it contains wood fractions of all sizes. Heilmann-Clausen (2004) studied the importance of differing size dead wood fractions (logs and snags) for fungal diversity in Danish forests and concluded that retaining whole

dead trees above a certain size was more likely to sustain a wider range of fungal diversity than a similar volume of smaller diameter dead wood, as the full array of coarse woody debris habitats (log, stump and branches of different dimensions) was represented. The same conclusion can be drawn from this study, with a large, older living tree containing a wide range of wood fractions which support a higher degree of saproxylic beetle diversity than a smaller, younger living tree.

5.5 Summary

Living *E. obliqua* trees host a high diversity of saproxylic beetle species. The oldest trees hosted a greater number of species and a higher number of unique species than the younger trees for both un-standardised datasets and for datasets standardised by surface area sampled. The stem wood fraction had the most pronounced variation in saproxylic beetle diversity between the different aged trees, with significantly more obligate beetle species and a different assemblage of obligate beetle species found in the stems of the old trees. The high degree of saproxylic beetle diversity within the stem of an older tree is though to be linked with an increase in dead wood or suitable habitat (wood decay) within the stem of the older trees (this is supported by findings in Chapter 6). While younger trees are also important for saproxylic beetle diversity, this study highlights the importance of older trees as they support a suite of species that cannot be found in younger trees, and that are entirely dependent on dead wood for their continued existence. It also highlights that old eucalypt trees in Tasmania may be as important for saproxylic beetle biodiversity as certain old trees in Europe.

Appendix 5.1 MRPP values for each pair-wise comparison of saproxylic beetles captured by emergence trapping of stems (wood and bark) and branches from three age-classes. Significant values are shown in bold (p > 0.05).

Tree Age-Wood Fraction Comparison	*Complete Dataset*	*Standardised Dataset*
Young-Stem vs Young-Branch	**0.001**	**0.016**
Young-Stem vs Medium-Stem	0.070	**0.042**
Young-Stem vs Medium-Branch	**0.008**	0.089
Young-Stem vs Old-Stem	**0.004**	**0.007**
Young-Stem vs Old-Branch	0.415	0.808
Young-Branch vs Medium-Stem	**0.004**	**0.067**
Young-Branch vs Medium-Branch	**0.018**	0.388
Young-Branch vs Old-Stem	**0.002**	**0.017**
Young-Branch vs Old-Branch	**0.038**	0.395
Medium-Stem vs Medium-Branch	0.070	0.083
Medium-Stem vs Old-Stem	0.426	0.724
Medium-Stem vs Old-Branch	**0.050**	**0.025**
Medium-Branch vs Old-Stem	**0.004**	**0.014**
Medium-Branch vs Old-Branch	0.714	0.814
Old-Stem vs Old-Branch	**0.003**	**0.006**

Chapter 6

The interaction of tree age, rotten wood, wood-decay fungi and saproxylic beetles

6.1 INTRODUCTION

Older, larger diameter trees and logs have been found to host a different and often a more diverse assemblage of saproxylic beetles and wood-decay fungi than younger, smaller diameter trees and logs (Chapter 5; Grove *et al.* 2002; Hopkins *et al.* 2005; Jonsell *et al.* 1998; Kruys *et al.* 1999; Renvall 1995; Similä *et al.* 2003; Yee 2005). In particular, the larger wood fractions have been documented as a preferred habitat for many threatened or 'red-listed' saproxylic species (Alexander 2002; Bader *et al.* 1995; Renvall 1995; Sippola and Renvall 1999). A reason that older, larger-diameter wood fractions can support a different community of saproxylic species may be due to the generally more complex and varied microhabitats found within their interior (Speight 1989).

Different microhabitats often develop within trees or logs through the action and succession of decomposer or wood-boring organisms such as wood-decay fungi, bacteria and invertebrates (Dajoz 2000; Käärik 1974; Speight 1989; Swift 1977). Older, larger diameter wood fractions have a larger surface area that allows more individuals to colonise the wood, and as they are older they are more likely to have been exposed to more stochastic events that cause damage. These may provide entry points for wood decay fungi, saproxylic beetles and other invertebrates (Adkins 2006). Each damage event will be associated with a different set of environmental conditions, which creates an opportunity for different species of fungi and invertebrates to colonise the wood. These in turn can provide the appropriate conditions for other organisms to also colonise the wood, and hence many different successional pathways can be followed (Heilmann-Clausen and Christensen 2004; Käärik 1975; Komonen 2003; Niemelä *et al.* 1995; Speight 1989). The action of different species alters the physical and chemical properties of the wood in different ways (Swift 1977), resulting in wood in various states and types of decomposition, which can be classified into different rotten wood types.

The term 'rotten wood' is used as it includes any wood that has been structurally altered, whether by feeding insects, or by wood decay fungi. The term 'decayed wood' refers more specifically to wood that has been decomposed by enzymes produced by wood-decay fungi.

Saproxylic organisms, such as wood-boring beetles, termites and wood decay fungi, can have close associations with a rotten wood type. These associations can range from the simple, where the organism is directly involved in the creation of the rotten wood (e.g. the comminution of wood by longicorn (Cerambycidae) beetle larvae) to more complex interactions (Müller *et al.* 2002). Some beetle species can be associated with the rotten wood by having an association with the causal organism. For example, some beetle species rely on certain fungi present in the wood for water or nutritional elements such as specific vitamins; or require the wood to be altered by the fungi before it is suitable for consumption, for instance certain fungi can detoxify the wood by breaking down toxins and repellent allelochemicals (Müller *et al.* 2002; Swift and Boddy 1984). Fungi also decompose the wood making it easier for the beetle to chew and assimilate (Hanula and New 1996; Kukor and Martin 1987; Müller *et al.* 2002; Swift and Boddy 1984). Other beetle species are predators of invertebrates that utilise the rotten wood. For example, the European click beetle (Elateridae) *Elater ferrugineus* is a predator of scarabaeid beetles that occur in red rotten wood (Svensson *et al.* 2004).

Associations between beetles and rotten wood types have been previously found in *E. obliqua* logs (Yee 2005). Yee (2005) studied large and small logs in an intermediate decay stage and identified eleven rotten wood types. She found that some rotten wood types, such as inner heartwood brown rots, occurred more often in larger logs, and were thought to have their origin within the standing tree. Several beetle species, such as the zopherid *Pycnomerus* TFIC sp 02 and the prostomid *Prostomis atkinsoni*, seemed to 'prefer' these inner heartwood brown rots. Other studies have also found beetle associations with either brown or white rots (Araya 1993). Brown or white rots are two broad decay types caused by fungi breaking down different chemical components in the wood. Brown rot is formed when only the cellulose and hemicellulose is degraded; white rot involves the decomposition of all cell wall components (i.e. lignin, cellulose and hemicellulose) (Rayner and Boddy 1988; Swift 1977).

Stem-dwelling beetles accounted for much of the distinctiveness of the saproxylic beetle fauna of trees in the oldest age-class (Chapter 5). A suggested reason for this was a higher complexity of habitats present within older stems compared to stems of trees in the two younger age-classes. This chapter investigates whether older, large diameter trees have different and more complex rot communities than younger, smaller trees and hence whether this supports the explanation of saproxylic beetle diversity differences between the oldest and younger age-classes. It also explores associations between some beetle species and rotten wood types, which may in turn assist in the explanation of some of the beetle preferences for a tree age-class as described in the Chapter 5. Questions raised by Yee's (2005) research concerning the origin of inner heartwood rots in logs are also addressed.

6.2 METHODS

Data Collection

Beetle abundance data were collected by destructive sampling and emergence trapping of wood billets cut from the stems of eighteen *E. obliqua* trees, six trees from each of three age-classes: 69 years old (young trees); 105 years old (medium age trees); and > 150 years old (old trees). For full details of the study site and sampling methods see Chapter 2.

In summary, eighteen trees were randomly chosen and felled from along two transects. Pairs of wood billets were cut from each stem at three standard heights (11m – 12 m above ground-level; immediately below the crown; and within the live crown) (see Figure 2.1). Two half-metre long billets were sampled from medium-aged and old trees; and two one-metre long billets were sampled from younger trees. A longer billet was taken for the younger trees to increase the amount of wood sampled, given their small diameter.

For one billet of each pair the upper cut face was photographed, and the patches of decay (i.e. decay columns) were labelled and recorded. Samples of each type of decay per face were collected for further analysis. This included categorising the decay type (outlined below) and the isolation of any associated wood decay fungi for a separate study conducted by Anna Hopkins (2006).

For each wood billet the bark was then separated from the stem and the billet placed in a separate emergence trap made of fine mesh. Beetle emergence was monitored for eighteen months. After this time the wood billet was destructively sampled as outlined below.

The remaining billet from each pair was destructively sampled for beetles by splitting the wood into small pieces using a tomahawk and mallet. The billet was then intensively searched, and any beetles located were collected by hand. This method follows techniques developed and adopted locally by Yee (2001). Detailed records were taken of the habitat of any beetles captured; this included the rotten wood type (wood pieces were collected for further analysis) and location within the stem (for example sapwood or heartwood). All collected beetles were mounted and identified to morphospecies (Oliver and Beattie 1996a).

Data Analysis

Classification and description of rotten wood types

All rotten wood samples collected were classified into preliminary groupings based on the rot colour, texture (such as blocky, stringy, pocketed or spongy) and suspected causal agent (fungi, insects or mechanical damage). Other identifiers included the wetness of the wood and the presence and colour of fungal mycelium. The preliminary groupings were refined by comparison with samples collected and described by Yee (2005). These rotten wood samples were collected from *E. obliqua* logs of various stages of decay in southern Tasmania, and assisted the classification of the rot samples from this study by providing information on the degree of variation within a rotten wood type. The terms '*rotten wood*' and '*rotten wood type*' as suggested by Yee (2005) are used rather than '*decayed wood*' and '*decayed wood type*' as the causal agent for some of the rot types was not fungal. The location of each rotten wood type was classified into sapwood, outer heartwood or inner heartwood, depending on the location from which it was most frequently sampled.

Comparing rotten wood types per age-class

The mean number of rotten wood types for each age-class was calculated by pooling the data for each tree. Any significant difference in means was tested using a one-way analysis of variance (ANOVA) and follow-up multiple comparison tests (Ryan-Einot-Gabriel-Welsch Multiple Range Test: REGW test) in SAS 9.1 (Anon. 2002). The difference in the frequency of different rotten wood types between tree age-classes was tested using Chi-square analysis in Excel (Microsoft 1997).

Measuring the amount of decay

The amount of decay in each tree was measured by digital interpretation of photographs of the three cut faces at each standard sampling point using SigmaScan Pro 4.0 (Jandel Scientific 1987-1996). The scale of each photograph was calibrated with reference to a 10 x 20 cm white board included in the photograph. A representation of the average amount of decay in each tree was calculated by determining an average of the area of decay for the three cut faces at each of the three standard sampling points. This was then expressed as a proportion of the surface area of the cut face at each standard sampling point (%). Differences in proportion of decay between tree age-classes were compared using one-way analyses of variance (ANOVA) and follow-up multiple comparison tests (Ryan-Einot-Gabriel-Welsch Multiple Range Test: REGW test) in SAS 9.1 (Anon. 2002).

Beetles and rot

Rotten wood and beetle abundance data from the destructive sampling of wood billets (one billet of each pair at time of felling and the remaining billet of each pair after eighteen months of emergence trapping) were analysed to investigate specific rot and beetle associations. A total of 22 species of saproxylic beetles and 334 individuals were collected as adults from the destructive sampling. The total number and mean number of species and individuals for each rotten wood type were calculated using data pooling from all trees sampled. The frequency of occurrence of each species collected from rotten wood was tabulated using data pooled across all trees.

Beetle assemblage composition and rotten wood composition for all three age-classes were compared using Non-metric Multidimensional Scaling (NMS), an unconstrained ordination technique, and Multi-Response Permutation Procedures (MRPP), using PC-ORD version 4 (McCune and Mefford 1999). Rotten wood data were presence/absence per tree and beetle data were abundance per tree (combined emergence trapping and destructive sampling data) and $\log_{10}(x + 1)$ transformed. The NMS was calculated using a Sorenson (Bray-Curtis) distance measure, choosing the 'slow and thorough autopilot' mode. Vectors defined by beetle abundance and rotten wood presence/absence data with $r^2 > 0.3$ were overlaid. Untransformed data were used for MRPP analysis and calculated using the recommended Euclidean distance measure.

Mantel tests were performed in PC-ORD version 4 (McCune and Mefford 1999) to determine whether the patterns of beetle assemblage composition were similar to the patterns of rotten wood in the same trees. Beetle assemblage composition was based on abundance per tree. To test whether the distribution of obligate or facultative saproxylic species behaved differently with regard to rotten wood distribution, the beetle species were divided into two groups (obligate and facultative), based on their degree of dependence on dead wood. Rotten wood distribution was investigated in several ways: presence/absence of rotten wood per tree; presence/absence of decayed wood per tree (only includes rotten wood types that are associated with fungi and therefore excludes discoloured wood, termite damage and cerambycid larva damage); mean proportion of the sampled surface area that was rotten wood per tree; mean proportion of the sampled surface area that was decayed per tree; and presence/absence of each rot type per tree. The Mantel tests gave p values based on randomisation (Monte Carlo) tests using 1000 randomised runs.

Beetles and fungi

Mantel tests were performed in PC-ORD version 4 (McCune and Mefford 1999) to determine whether the patterns of beetle assemblage composition within a tree were similar to the patterns of wood decay fungal distribution. The fungal data were obtained from the same (or adjacent) wood billets as the beetle abundance data by

Anna Hopkins (University of Tasmania) (see Chapter 2 and Figure 2.1 for additional details). Beetle assemblage composition was based on abundance per tree. To test whether the distribution of obligate or facultative saproxylic species behaved differently from fungal distribution, the beetle species were divided into two groups, based on their dependence on dead wood.

6.3 RESULTS

Classification and description of rotten wood types

Eleven different rotten wood types were identified from the 18 *E. obliqua* trees sampled in this study (Table 6.1). A detailed description including photographs of each rotten wood type can be found in Appendix 6.1. No soft rots were found. One rotten wood type, termite wood, was found in sapwood. All other rotten wood types were only found in the heartwood. Some rotten wood types were found to occur more often in either the inner heartwood or outer heartwood. The white rots were found most frequently in the inner heartwood and the brown rots were located throughout the heartwood. The wet brown cubic rot and dry brown cubic rot was often found in localised patches in the outer heartwood. The main suspected causal agent for nine rotten wood types was fungal, while two rotten wood types were probably caused by insect activity. Three rotten wood types, discoloured wood, red brown blocky fibrous rot and brown mudgut rot were similar to those found in logs by Yee (2005). The brown cubic rot identified by Yee (2005) from logs was similar to both the dry brown cubic rot and wet brown cubic rot sampled from trees. As there was a clear difference in moisture content between these two rotten wood types they were classed separately.

Table 6.1 Rotten wood types identified from 18 E. obliqua trees and their comparison with rotten wood types collected by Yee (2005) from E. obliqua logs.

Rotten wood type	Suspected main decomposition agent*	Rot type	Rot Location[#]	Brief description	Related rotten wood type in Yee (2005)
Discoloured wood	Fungi, possibly bacteria	N/A	N/A		Discoloured wood
Termite Damage	Insects (termites)	N/A	Sapwood/Outer Heartwood	Smoothed termite galleries	-
Cerambycid Larva Damage	Insects (cerambycid beetle larvae)	N/A	Outer and Inner Heartwood	Large string frass	-
Stringy Rot	Fungi	White	Inner Heartwood	Brown and very fibrous.	-
White Spongy Rot	Fungi	White	Inner Heartwood	Very bleached, soft but also quite stringy in places.	-
Small Pocket Rot	Fungi	White	Inner Heartwood	Pockets very small and dispersed. Mycelium often visible in wood grain.	-
Combination Pocket and Brown Rot	Fungi	White and brown together	Outer and Inner Heartwood	Looks like a pocket rot and a brown cubical rot both growing together.	-
Dry Brown Cubic Rot	Fungi	Brown	Outer Heartwood	Crumbly, cubical decay, consistently very dry and light coloured even in newly fallen trees.	Brown Blocky Crumbly Rot
Wet Brown Cubic Rot	Fungi	Brown	Outer Heartwood	As above but consistently wetter even in newly fallen trees.	Brown Blocky Crumbly Rot
Red Brown Blocky Fibrous Rot	Insects, fungi	Brown	Outer and Inner Heartwood	Blocky and fibrous, often very wet with a reddish colour	Red Brown Blocky Fibrous Rot
Brown Mudgut Rot	Insects, fungi and other	Brown	Inner Heartwood	Wet mud-to-clay like consistency often occurring near wet brown cubic rot	Brown Mudgut Rot

*Adapted from Yee (2005).

[#] Location where rotten wood type was most frequently found.

Tree age and rotten wood distribution

The old trees had a significantly higher number of rotten wood types (Figure 6.1) and area of stem decayed (Figure 6.2), than the two younger age-classes. The medium-aged trees had a significantly lower number of rotten wood types and area of stem decayed than the young trees.
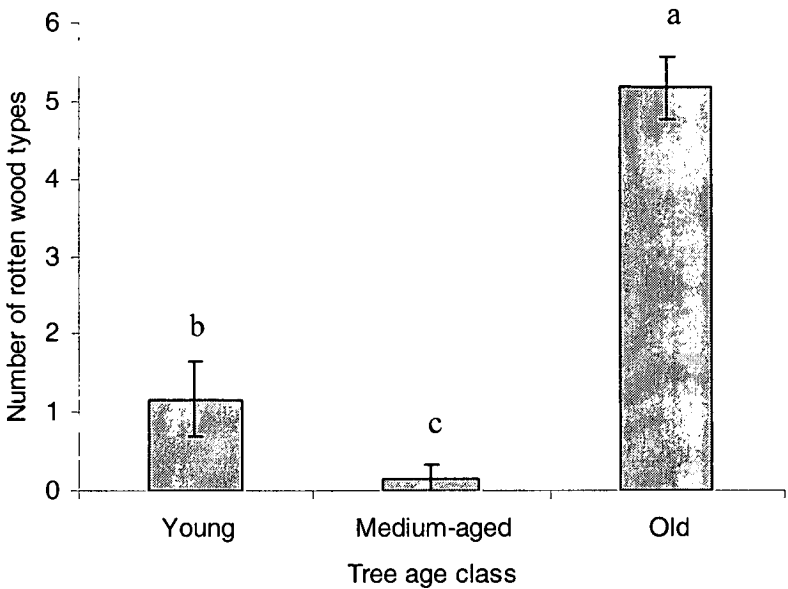
Figure 6.1 Mean number of rotten wood types per tree in each of three age-classes. Error bars show standard error, letters a, b and c represent significantly different (p<0.05) means from ANOVA.
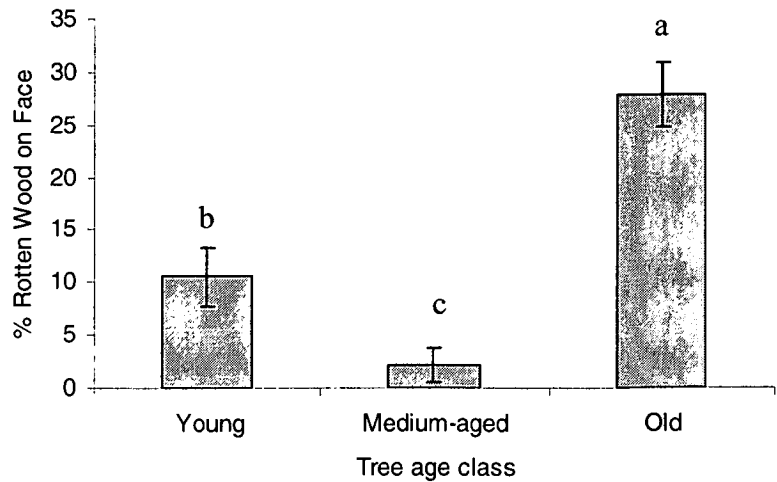
Figure 6.2 Mean percentage of rotten wood on each log section per age-class. Error bars show standard error, letters a, b and c represent significantly different (p<0.05) means from ANOVA.
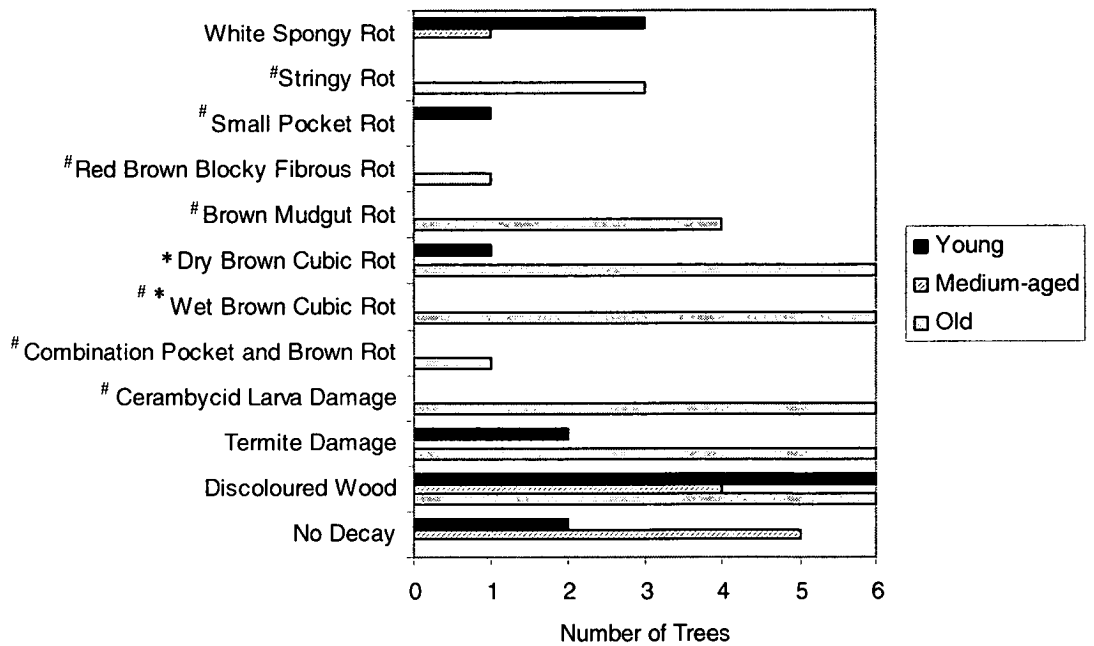
*Figure 6.3 Number of trees per age-class with each rotten wood type. * denotes rotten wood types that are significantly different in occurrence among the age-classes using Chi-square analysis (p<0.05) and # denotes those that are unique to an age-class.*

The rotten wood types varied considerably between each tree, particularly in the two younger age-classes. Two of the younger trees had no decay and only one medium-aged tree had decay present (Figure 6.3). Brown rots were more commonly found in the old trees, with all six old trees having dry brown cubic rot and wet brown cubic rot. Only one young tree was found to have a brown rot (dry brown cubic rot). White rots were more commonly found in the younger age-classes, with one medium-aged tree and three of the younger trees having white spongy rot and one of the younger trees having small pocket rot. Only one type of white rot, stringy rot, was found in the old trees, and only occurred in three trees. Rotten wood types caused by insects were mainly found in the old trees, with cerambycid larva damage and termite damage found in all of these trees. However, two of the young trees also had termite damage; decay was found also in these two trees. Seven of the rotten wood types were only found in one age-class each.

Beetles and rot

The brown rot types tended to have a higher total number of species and individuals of saproxylic beetles associated with them (Figure 6.4 a and b). However, when means are compared no significant difference is found between any of the rot types (Figure 6.4 c and d). Of the more commonly found saproxylic beetle species, higher numbers of species and individuals were associated with a brown rot type (Table 6.2).

Two prostomid species, *Prostomis atkinsoni* and *Dryocora cephalotes*, appeared to 'prefer' the two wetter brown rotten wood types (wet brown cubic rot and brown mudgut rot)(Table 6.2). Two curculionid species Cryptorhynchinae TFIC sp 02 and *Dryophthorus* ECZ sp 02 were also only found in the two wetter brown rot types, but less frequently. The lucanid *Syndesus cornutus* was only found in the brown cubic rots. The cerambycid *Toxeutes arcuatus*, curculionid *Pentarthrum* TFIC sp 03 and carabid *Trechimorphus diemenensis* were found only in the brown rots. Two species- the zopherid *Pycnomerus* TFIC sp 02 and curculionid *Cossonus* KH sp 01, did not appear to have a clear preference for either white or brown rots, occurring in both (Table 6.2 & 6.3). Three species were frequently found in tunnels in discoloured, yet solid wood. Only one species, *Cossonus simsoni*, occurred more frequently in association with white rots.
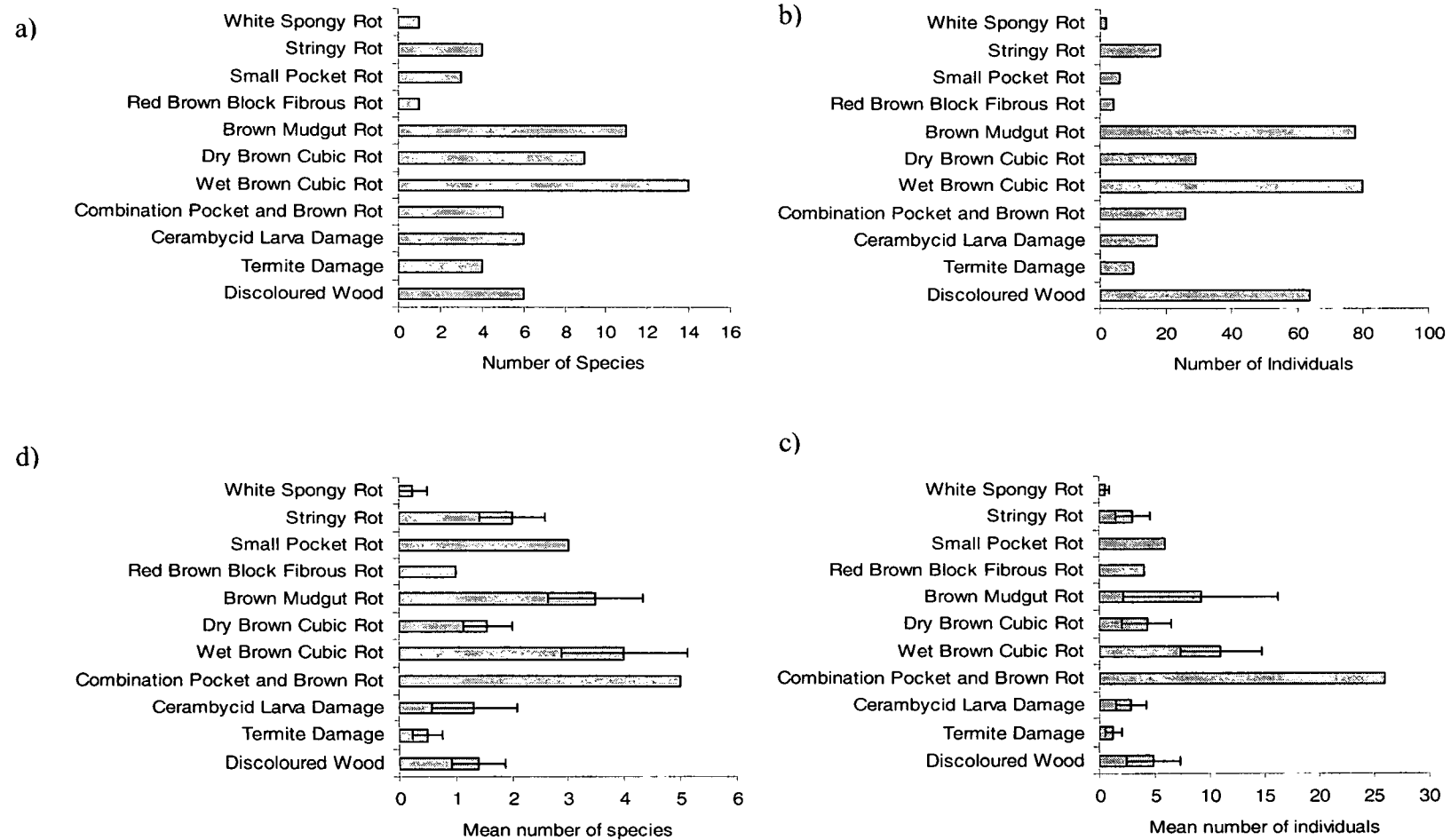
Figure 6.4 Bar graphs of saproxylic beetles collected from rotten wood showing total number of a) individuals and b) species for each rotten wood type, pooled across all trees; and mean number of c) individuals and d) species for each rotten wood type, per tree. Error bars show standard error.

Table 6.2 Species associated with rotten wood types as deduced from destructive sampling data. Species are listed in order of decreasing frequency. Apparent decay type is abbreviated as Wh- (white rot) and Br- (brown rot). The number within a cell is the number of trees in which the species was found, followed in brackets by the number of individuals collected. More than two occurrences are highlighted in bold. Species with fewer than two occurrences in total were omitted.

Rotten Wood Type	Discoloured Wood		Termite Damage	Cerambycid Larva Damage	Combination Pocket and Brown Rot	Wet Brown Cubic Rot	Dry Brown Cubic Rot	Brown Mudgut Rot	RBBF Rot	Small Pocket Rot	Stringy Rot	White Spongy Rot	
Apparent Decay Type	N/A		N/A	N/A	Wh/Br	Br	Br	Br	Br	Wh	Wh	Wh	
Tree Age-class	Young	Old	Old	Old	Old	Old	Old	Old	Old	Young	Old	Young	
Species Binomial													Total
Pycnomerus TFIC sp 02	**2 (7)**	**4 (20)**	1 (1)	3 (7)	1 (11)	**4 (9)**	1 (1)	**4 (11)**	1 (4)		**2 (13)**	1 (2)	24 (86)
Pentarthrum TFIC sp 03		**3 (17)**	1 (3)		1 (6)	**4 (12)**	1 (13)	**2 (2)**					12 (53)
Cossonus KH sp 01		**3 (5)**	1 (2)		1 (1)	**2 (3)**	1 (3)	1 (1)		1 (4)			10 (19)
Dryocora cephalotes				1 (3)		**4 (26)**		**3 (52)**			1 (2)		9 (83)
Prostomis atkinsoni					1 (7)	**3 (15)**	1 (1)	**4 (13)**					9 (36)
Syndesus cornutus						**5 (10)**	**3 (6)**						8 (16)
Trechimorphus diemenensis				1 (1)		1 (1)	1 (1)	1 (1)					4 (4)
Toxeutes arcuatus						1 (1)	1 (2)	1 (2)					3 (5)
Cossonus simsoni										1 (1)	**2 (2)**		3 (3)
Philothermus tasmanicus		1 (2)								1 (1)			2 (3)
Cryptorhynchinae TFIC sp 02						1 (1)		1 (1)					2 (2)
Dryophthorus ECZ sp 02						1 (1)		1 (1)					2 (2)

Table 6.3 Frequency of occurrence in emergence trapping of species that were apparently associated with any rotten wood types according to destructive sampling data. The number within a cell is the number of trees from which the species emerged, followed in brackets by the number of individuals collected.

Tree Age-class	69*	105	>150
Species Binomial			
Pycnomerus TFIC sp 02	1 (1)	0 (0)	5 (29)
Prostomis atkinsoni	0 (0)	0 (0)	4 (7)
Pentarthrum TFIC sp 03	1 (1)	0 (0)	4 (37)
Cossonus KH sp 01	1 (5)	0 (0)	4 (9)
Syndesus cornutus	0 (0)	0 (0)	4 (7)
Dryocora cephalotes	0 (0)	0 (0)	0 (0)
Toxeutes arcuatus	0 (0)	0 (0)	0 (0)
Cossonus simsoni	0 (0)	0 (0)	1 (2)
Trechimorphus diemenensis	3 (5)	3 (4)	5 (39)
Philothermus tasmanicus	2 (2)	3 (3)	2 (3)
Cryptorhynchinae TFIC sp 02	0 (0)	1 (1)	0 (0)
Dryophthorus ECZ sp 02	0 (0)	0 (0)	0 (0)

*All beetle species in this age class emerged from young trees that had white rot, either small pocket rot (Tree 24) or white stingy rot; or brown rot; dry brown cubic rot (Tree 41).

Table 6.3 details the emergence trap capture of the species commonly found associated with any rotten wood types (as listed in Table 6.2) . While no specific interactions between beetles and rotten wood type can be inferred from the emergence trapping data (as beetles were not directly found within the rotten wood type and most rotten wood pieces have more than one rotten wood type), the data tend to support the associations found using the destructive sampling data. For example, *Pycnomerus* TFIC sp 02 and *Cossonus* KH sp 01 were only found in young trees that also had a white rot (Table 6.3). *Pentarthrum* TFIC sp 03 was captured by emergence trapping from one young tree (Table 6.3). This is consistent with its 'preference' for brown rots indicated from the destructive sampling data, as the young tree also had brown rot (and was the only tree from the two younger age-classes with it). *Prostomis atkinsoni, Cossonus* KH sp 01, *Syndesus cornutus, Pentarthrum* TFIC sp 03 and *Pycnomerus* TFIC sp 02 frequently occurred in emergence traps from the oldest aged trees (which all had brown rotten wood types) and only occurred in younger trees that also had either brown or white rot.

The NMS ordination of the complete beetle data set and rotten wood types shows a clear, but incomplete separation of the beetle assemblages between the old trees and the two younger age-classes (Figure 6.5 a and b). This is supported by the MRPP result with a significant difference found beetle assemblage between the old trees
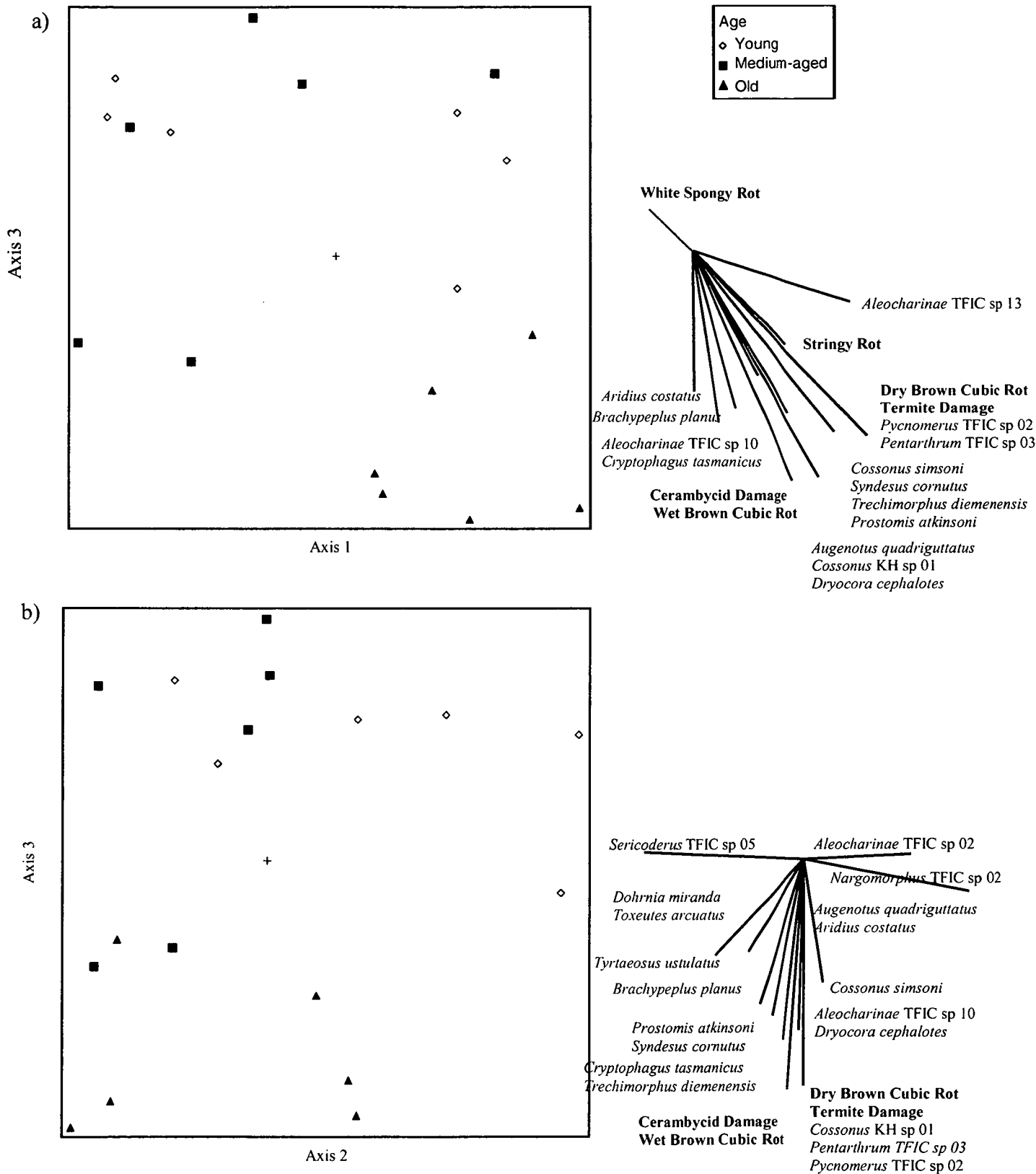
Figure 6.5 NMS ordination of saproxylic beetles captured by emergence trapping and destructive sampling of stem for each tree age-class showing axes 1 and 3 (a) and axes 2 and 3 (b). Vectors ($r^2 > 0.3$) are defined by beetle abundance and presence/absence of rotten wood type; for greater clarity these are shown adjacent to the ordination. Abundance data were $log_{10}(x+1)$ transformed. Stress = 9.28 MRPP p = 0.002

and two younger age classes ($p = 0.002$). There is no clear separation (Figure 6.5 a and b) or signifcant difference (MRPP, $p = 0.35$) between the younger two age-classes. The vector overlay shows several beetle species and rotten wood types to be correlated with the older trees.

Table 6.4 Tree level beetle assemblage composition compared with rotten wood distribution, or decay wood distribution, or fungal assemblage composition and tested using a Mantel test. Significant results are highlighted in bold.

| | Beetle Species Dataset | | | | | |
| | All Species | | Facultative Species | | Obligate Species | |
Comparison Dataset	*r*	*p*	*r*	*p*	*r*	*p*
Presence/absence of any rotten* wood per tree	0.105	0.284	-0.028	0.452	**0.282**	**0.002**
Presence/absence of any decayed* wood per tree	**0.317**	**0.005**	0.065	0.155	**0.551**	**0.001**
Mean proportion of billet face that is rotten wood per tree	**0.263**	**0.002**	0.087	0.141	**0.428**	**0.001**
Mean proportion of billet face that is decayed wood per tree	**0.393**	**0.001**	0.117	0.066	**0.614**	**0.001**
Presence/absence of individual rotten wood type per tree	**0.410**	**0.001**	0.087	0.128	**0.692**	**0.001**
Presence/absence of individual decayed wood type per tree	**0.360**	**0.002**	0.063	0.214	**0.612**	**0.001**
Fungal assemblage composition per tree	0.116	0.096	0.039	0.323	**0.166**	**0.036**

* Rotten wood includes all rotten wood types; decayed wood refers to those where the suspected main causal agent is fungal and therefore excludes discoloured wood, termite damage and cerambycid larva damage.

The presence or absence of rotten wood within a tree did not significantly correlate with the assemblage composition of all beetle species or with the assemblage composition of facultative saproxylic beetle species (Table 6.4). Assemblages of obligate beetles were weakly, but significantly correlated with the presence or absence of rotten wood within a tree. When the presence or absence of decayed wood (rotten wood type associated with fungi) was compared, the correlation for all beetle, facultative and obligate beetle assemblages slightly increased. However, the correlation for facultative beetle assemblages was still not significant. The mean proportion of the sampled surface area that was rotten wood and decayed wood had a slightly stronger correlation with the assemblage composition of all species, facultative species and obligate species, than did the presence or absence of rotten wood or decayed wood. The strongest correlation was found between the obligate beetle assemblage composition and the community of particular rotten wood types (measured as presence or absence) within each tree. Facultative saproxylic beetle

assemblage composition was not significantly correlated with any of the rotten wood or decayed wood comparison datasets.

Beetles and Fungi

Neither the assemblage composition of all beetle species, nor that of facultative saproxylic species, was correlated with the assemblage composition of fungal species (Table 6.4). Obligate beetle assemblage composition had a very weak but significant correlation with fungal assemblage composition. In a Mantel test, fungal assemblage composition was also weakly but significantly correlated with the presence/absence of rotten wood types within each tree ($r = 0.219$, $p = 0.015$).

6.4 DISCUSSION

Rotten wood classification

This study of 18 *E. obliqua* living trees has identified 11 different rotten wood types. Table 6.5 compares these rotten wood types to others collected from *Eucalyptus spp.* logs and trees from various studies. As the classification system used in this study was based on that developed by Yee (2005) (with all rotten wood types collected from this study being compared both to the extensive descriptions and images provided in Yee (2005) and directly to rotten wood samples collected by Marie Yee) rotten wood relationships between the two studies may be considered to be reliable. However, the reliability of the relationships of the rotten wood types from the current study to the other studies listed in Table 6.5 is tentative.

The rotten wood classification developed by Yee (2005) has been enhanced by the inclusion of two rotten wood types directly relating to insect activity (termite damage and cerambycid larva damage). Yee (2005) suggested that various invertebrates may be involved in the formation of two rotten wood types (discoloured wood and brown mudgut rot) but did not identify the invertebrate groups involved. The more advanced state of rot in the logs studied by Yee (2005) may have obscured the differentiation of rotten wood types caused by insect activity.

Table 6.5 Classification of the eleven rotten wood types from this study compared with classifications from other studies. Rotten wood types in the same rows are thought to be the same. Adapted from Hopkins (2006) and Yee (2005). Rot location is shown when identified in study. Abbreviations: S-surface, IH-inner heartwood, OH-outer heartwood and H-both outer and inner heartwood.

This study, *E. obliqua* trees, Tasmania	Yee (2005) *E. obliqua* logs, Tasmania	Meggs (1996) *Eucalyptus* spp., Tasmania	Refshuage, *E. regnans* trees, Victoria	Tamblyn (1937) *E. marginata* trees, Western Australia	Parkin (1942) *E. regnans,E. viminalis* trees & logs, Victoria
Discoloured wood (H)	Discoloured wood (H)				
Termite Damage (S, OH)					
Cerambycid Larva Damage (H)					
Stringy Rot (IH)					
White Spongy Rot (IH)				Yellow straw rot	White spongy rot
Small Pocket Rot (IH)			Small white pocket rot		Small white pockets
	Fibrous surface rot (S)	Soft yellow fibrous rot			Yellowish stringy rot
	White jelly surface rot (S)	Other (including wet jelly rot and blue stain fungi)			
	White pocket rot (OH)		Large white pocket rot Small brown pocket rot Brown stain associated with small white pocket rot	White pocket rot	White pocket rot
	White stringy rot (OH)		White spongy rot Large white pocket rot of stringy type		White stringy rot
	Yellow dry slatey rot (OH)				
Combination Pocket and Brown Rot (H)					
	Brown cubic friable rot (OH)				
Dry Brown Cubic Rot and Wet Brown Cubic Rot (OH)	Brown blocky crumbly rot (IH)	Orange/red/brown crumbly rot	Brown cubical rot	Brown trunk rot Xylostroma heart rot	Brown cubical rot
Red Brown Blocky Fibrous Rot (H)	Red brown blocky fibrous rot (IH)	Red blocky rot Red blocky rot with white fungal hyphae			Yellow brown spongy rot
Brown Mudgut Rot (IH)	Brown mudgut rot (IH)	Orange/red clayey rot			

Of the 11 rotten wood types identified by Yee (2005) in logs and the 11 rotten wood types identified in trees in this study, only five rotten wood types are common to both studies (Table 6.5). This includes the two brown cubic rots (wet and dry) which were differentiated in this study. All of these shared rotten wood types were brown rots and located within the heartwood of trees and logs (with the exception of discoloured wood) (Table 6.1 and 6.5). This supports the theory presented by Yee (2005), who suggested that the inner brown heartwood rots in logs were present at the time of tree fall, while many of the surface and outer rots (typically white rots) occurred subsequent to tree fall. This is discussed further in relation to tree age in the next section.

Associations between tree age and rotten wood

A clear difference in the quantity and type of rotten wood present was found for the different tree age-classes. Old trees had a complex distribution of rotten wood, with all having 4-6 different rotten wood types per stem, and on average almost a third of the wood face was rotten. Six rotten wood types were only found in the old trees. In contrast, the two younger age-classes were less complex: two of the young trees had no decay at all, while four had 1-3 rot types occurring per tree; and on average only 10% of the face was rotten. The medium-aged trees had the simplest rot distribution, with only one type of rotten wood, in total, in only one tree. The increased complexity of rotten wood types, which it appears have been formed through the action of a different suite of decomposer organisms in old trees, is consistent with the general assumption that older trees have a high diversity of microhabitats.

Older trees are more likely to have rotten wood within the heartwood, as they have an increased chance of been exposed to events and conditions that allow colonisation of decomposer species to occur. Damage from events such as wildfires and windstorms and the activity of wood-boring invertebrates can create entry points for fungal and faunal communities that bypass the more protective bark and sapwood layer, providing direct access into the heartwood of a tree (Greaves *et al.* 1967; Perry *et al.* 1985; Tamblyn 1937; Wardlaw 2003; Wilkes 1985a, 1985b). The heartwood, which has few living cells, is generally easier to colonise than the

sapwood, which has functional cells that can actively defend, such as by the secretion of antibiotic compounds that inhibit decay (Rayner and Boddy 1988; Wilkes 1985a). Each damage event will have its own unique set of environmental conditions, which can favour the colonisation of different fungal and invertebrate species, and can create different rotten wood types within the tree. Older trees also have a larger amount of heartwood available than younger trees, which can allow more individual species to colonise and decompose the wood (Heilmann-Clausen and Christensen 2004).

The old trees in this study had survived at least two documented wildfire events (Alcorn *et al.* 2001; Hickey *et al.* 1998), and all such study trees possessed numerous fire scars (detailed in Chapter 2), which may have been entry points for decomposer organisms (Elliott and Bashford 1984; Perry *et al.* 1985; Wilkes 1985b). In addition, all of the old study trees also had many larger diameter branches (both dead and alive), which are known to provide useful infection courts (Tamblyn 1937; Wardlaw 2003). Termites and wood-boring cerambycid larvae were found to have caused extensive damage to the heartwood of all of the old study trees. These invertebrates may be more prevalent in older trees as they are utilising entry points, created by damage events, as outlined above, or they may have directly entered through the protective bark and sapwood into the heartwood by their own actions (Allison *et al.* 2004; Elliott and Bashford 1984; Elliott and de Little 1984; Kalshoven 1963; McCaw 1983; Perry *et al.* 1985; Speight 1989; Wilkes 1985b). The activity of these invertebrates can facilitate the colonisation (by providing entry points) and spread of other decomposer organisms within the stem. Hence it is likely that the presence of termites and wood-boring cerambycid larvae is another factor contributing to the quantity and complexity of rotten wood found within the stems of the old study trees.

The young trees had a consistently higher quantity and diversity of rotten wood than did the medium-aged trees. All trees were sampled from a mixed-age forest, and it is theorised that the young trees were suppressed by the older, dominant trees. Suppression can increase susceptibility to decay or to insect damage (Greaves and Florence 1966; Speight 1989). The young trees had developed only a very small girth for their age (detailed in Chapter 2), supporting this idea of suppression. Termite damage was found in two of the decayed trees, which may indicate a poor

ability to resist sapwood attack (Elliott and Bashford 1984; Greaves and Florence 1966). Termite activity also may have facilitated the colonisation and spread of decay (Coyle 1974), as the two trees with termites also had the highest amount of rotten wood. Alternatively the termites may be present due to the presence of decay (Perry *et al.* 1985). Other stem-boring invertebrates such as hepialid moths and cerambycid beetles have been found by a previous study to be a common source of decay column initiation in young eucalypts in wet eucalypt forests (Wardlaw 1994). The medium-aged trees appeared to be healthy with few signs of damage. No fire scars were found on any of these trees even though they had survived one documented severe wildfire (see Chapter 2) (Alcorn *et al.* 2001; Hickey *et al.* 1998). This low level of damage and lack of obvious physiological stress may explain the small amount of rotten wood found within these trees.

White rot types were more prevalent in the younger aged trees and brown rots more prevalent in the old trees. These findings support those by Wardlaw (1997) who studied *Eucalyptus spp.* in Tasmania's wet forests and found that younger trees typically supported white rot but not brown rot. A similar pattern of brown rotten wood distribution was found in *E. obliqua* logs by Yee (2005), where brown rotten wood types were found preferentially in the heartwood of larger diameter logs, whose origin would have been older, larger diameter trees. The smaller diameter logs were more often associated with white rotten wood types in the sapwood or outer heartwood. Equivalent brown rot types were found in the heartwood of living trees in this study and logs in Yee (2005). Generally more advanced stages of these rotten wood types were found in logs, with more incidences and larger areas of less structured rotten wood types such as brown mudgut rot (Yee, *pers. comm.*).

The overlap of brown rots in old trees and large diameter logs supports Yee's (2005) suggestion that the brown heartwood rot types in logs originated within the heartwood of the living tree. The white rot types found in the living trees were quite different from those found in logs. In logs, the white rotten wood types generally occurred in the sapwood and outer heartwood, and were thought to occur once the log had fallen and the sapwood was no longer functional, whereas in trees the white rot types were found in the inner heartwood.

Beetles and rot

Some beetle species from this study seemed to 'prefer' certain decay types (either white or brown) and/or rotten wood types with similar characteristics. For example, both prostomid species *Prostomis atkinsoni* and *Dryocora cephalotes* were more frequently found in the wetter brown rots (wet brown cubic rot and brown mudgut rot). This is consistent with findings from a study that investigated beetle and rotten wood associations in *E. obliqua* logs by Yee (2005) (Table 6.5). As in the current study, she found no specific beetle associations with any particular rotten wood type, but she did find associations with an overall decay type (i.e. white or brown) and with rotten wood types with similar characteristics (e.g. wetter or cubic). Beetle and decay type associations in logs were consistent for most species frequently collected from trees. However, from this study *Cossonus simsoni* was only found in white rots and only in low numbers, but Yee (2005) found the species in both white and brown rots with a preference for brown rot types. It is likely that brown rot types, particularly in late stages, are the preferred substrate, as *Cossonus simsoni* was also found in large numbers in very decomposed (almost humus-like) wood in the base of *E. obliqua* trees (unpresented data: 283 individual *Cossonus simsoni* beetles were collected (often as fragments) from the very decomposed heartwood that had been collected from the cross-section of stem exposed by felling for three >150 year old *E. obliqua* trees).

A few of the species frequently found in this study associated with rotten wood in *E. obliqua* trees were not found in logs. These species may prefer the earlier decomposition stage that is found in trees, or have some other habitat requirement that is provided by trees. For example, the two xylophagous cossonine species (*Cossonus* KH sp 01 and *Pentarthrum* TFIC sp 03), which were only found in trees, were associated with solid discoloured wood, as well as with brown rotten wood. These two beetle species may be involved in the initial colonisation and early decomposition stages of *E. obliqua* trees. The larvae and/or adults of these two species are thought to have the ability to bore through solid wood, as other members of the genera have been documented as wood-boring (Haack, 2006) and in this study the species were found within tunnels in solid wood. Both species were also found in two of the youngest trees with decay and were frequently captured from artificially mechanical wounded or burnt trees (Chapter 7).

Table 6.5 Comparison of 'preferred' rotten wood habitats of saproxylic beetles from E. obliqua trees and logs. Decay types that beetles were collected from are listed, with the 'preferred' decay type in bold.

Species Binomial	This study, E. obliqua *trees* Decay Type	Notes	Yee (2005), E. obliqua *logs* Decay Type	Notes
Pycnomerus TFIC sp 02	*White/Brown*		*White/Brown*	
Prostomis atkinsoni	*Brown*	*Wet types*	*White/Brown*	
Pentarthrum TFIC sp 03	*Brown*		*N/A*	
Cossonus KH sp 01	*White/Brown*		*N/A*	
Syndesus cornutus	*Brown*	*Cubic Rots*	*Brown*	*Cubic/Crumbly rots*
Dryocora cephalotes	*White/Brown*	*Wet types*	*Brown*	
Toxeutes arcuatus	*Brown*		*Brown*	
Cossonus simsoni	*White*		*White/Brown*	
Trechimorphus diemenensis	*Brown*		*White/Brown*	
Philothermus tasmanicus	*White*		*White/Brown*	
Cryptorhynchinae TFIC sp 02	*Brown*		*N/A*	
Dryophthorus ECZ sp 02	*Brown*		*N/A*	

Some of the beetle species common to the brown rotten wood in trees and logs may have remained within the heartwood, as the tree passed through its successional stages from the standing living tree to the downed log. It is likely that this could occur for *Prostomis atkinsoni, Dryocora cephalotes* and *Pycnomerus* TFIC sp 02. Yee (2005) suggested that two of these species (*Prostomis atkinsoni and Pycnomerus* TFIC sp 02) were capable of successive generations within the logs without emerging; this is likely to be the case for *Dryocora cephalotes* also. All three beetle species were commonly found aggregated with both larvae and adults living within the same wood in both logs and trees. Significantly more of these beetles were sampled in trees *in-situ* by destructive sampling than emerged over 18 months (Chapter 3), and both adults and larvae were found still alive in the wood after 18 months of emergence trapping. Similar results were found by Yee (2005) for *Pycnomerus* TFIC sp 02, which survived in original host material for 25 months in the laboratory. A study on *Prostomis atkinsoni* found that individuals were genetically similar at fine spatial scales (Watson 2003), which also suggests low dispersal rates. The apparently low dispersal rates and preference for a relatively stable habitat within old, large diameter trees and logs is not only interesting in terms of the ecology of the beetle species, but it also indicates their potential vulnerability to habitat loss due to forest industry operations that reduce the quantity of large diameter trees in the landscape. These three species are closely related to

beetle species in Europe that have had drastic declines in population and range, with some regional extinctions occurring (see Chapter 5).

Yee (2005) found many more species (37) commonly associated with rotten wood in logs than this study found to be the case for trees (12 species). This may be due to the greater sample size (42 logs sampled compared to the 18 trees in this study), more advanced decay stage and different types of rotten wood present (sapwood rotten wood types were frequently found in logs, as well as heartwood rots). In general, she found the brown heartwood rot types and surface/sapwood to be associated with significantly more beetle species. Brown mudgut rot was the most favourable microhabitat for beetles, while the two white rotten wood types (white pocket rot and white stringy rot) were the least favourable microhabitats. Similar trends were found for beetles within trees (although no significant differences were found), with the brown rot types generally having a higher number of species and individuals. White spongy rot was one of the least favourable habitats for beetles in trees, but small pocket rot was among the more favourable habitats when mean totals per tree were compared. This rotten wood type was only found in one tree, so the finding may not hold if more samples were compared.

While the destructive sampling allowed the investigation of direct associations between some beetle species and rotten wood types, it had a limited capacity to capture some beetle species, with far fewer species captured by destructive sampling than those caught using emergence traps. Small, cryptic species were often missed and the majority of beetle species were only present as larvae, which are difficult to identify and were excluded from this study. Correlation analysis of the combined beetle datasets from emergence trapping and destructive sampling with the rotten wood types per tree allowed a broader investigation of beetle and rot type associations. The strong significant correlation between the assemblage composition of obligate beetle species (collected by both trapping methods) and rotten wood distribution suggests that additional species than those found by destructive sampling alone are associated with rotten wood.

The strong correlation that was found between obligate beetle assemblage composition and rotten wood distribution further supports the finding that old trees supported significantly more and differing assemblage composition of obligate saproxylic beetle species than did younger trees (discussed in Chapter 5). It was

proposed that this difference was due to old trees having both a greater quantity of habitat and a more suitable habitat within their stems (e.g. rotten wood). As discussed in the previous section, old trees have significantly more rotten wood and more rotten wood types, which supports this theory, but the additional strong correlation between obligate beetle distribution and rotten wood types demonstrates this interaction. While the presence/absence of rotten wood, and beetle distribution and amount of rotten wood, were correlated with obligate beetle assemblage composition, the strongest correlation was found with the distribution of the individual rotten wood types, thus highlighting the complex associations between beetles and rotten wood type (for example, from the general associations of decay type for brown rots and *Toxeutes arcuatus* to the more specific associations of brown cubic rots for *Syndesus cornutus*).

No significant association was found between rotten wood and facultative saproxylic beetle assemblage composition. This, however, does not mean that all facultative beetle species do not have an association with rotten wood, as associations for a few individual species would be overshadowed in the analysis. For example, the abundances of two facultative beetle species Aleocharinae TFIC sp 10 and *Cryptophagus tasmanicus* were positively correlated with the old trees and their vector overlays from the NMS ordination correspond with vectors of some rotten wood types.

Beetles and fungi

Obligate beetle species and fungal assemblage composition were weakly yet significantly correlated, suggesting an association between these organisms. Relationships between wood, fungi and beetles are complex and can range from the simple and direct (such as beetles grazing directly on the fungal mycelia) to the intricate and indirect (such as beetles only being able to utilise the wood after prior fungal attack, which alters the chemical defences and/or nutrient availability) (Crowson 1981; Kukor and Martin 1987; Müller *et al.* 2002; Rayner and Boddy 1988; Swift and Boddy 1984). Establishing relationships between beetles and wood decay fungi can be further complicated by the cryptic and often ephemeral nature of these organisms, particular the wood decay fungi. However, associations between

wood decay fungi and saproxylic beetles have been found in several other studies. Jonsell (2005) studied saproxylic beetles and aradid bugs in spruce high stumps in Sweden and found that the presence or absence of mycelia of two polypore species (*Fomitopsis pinicola* and *Trichaptum abietinum*) was the best explanatory variable for differences in invertebrate species composition. Lindhe (2004) also investigated saproxylic beetles in high stumps of spruce, birch, aspen and oak and found saproxylic species density was correlated with fungal diversity.

The correlation between obligate saproxylic beetles and fungal assemblage composition was considerably weaker than that between obligate saproxylic beetles and rotten wood types. One reason for this is that some of the rotten wood types (such as cerambycid damage) are directly caused by beetles, not by fungi. Another reason is the complex relationship that fungi have with wood. The decomposition of wood by fungi often involves a succession of species that alter the wood in various ways, with a rotten wood type often caused by the action of several fungi (Boddy 2001; Niemelä *et al.* 1995; Rayner and Boddy 1988; Renvall 1995). Often in advanced stages of decay the main causal wood decay species is no longer present. Thus, a fungus isolated from a rotten wood type may not be the causal organism.

6.5 Summary

Old, large diameter trees have a higher amount of decay and a greater diversity in rotten wood types than younger, smaller diameter trees. This higher diversity of microhabitats is linked with the high diversity of obligate saproxylic beetles associated with the stems of old trees (Chapter 5).

A high-degree of overlap of inner brown rotten wood types between trees and logs supports Yee's (2005) theory that these rot types developed within the living tree, prior to tree death. Old trees had numerous fire scars and large diameter branches, which may be useful infection courts for decomposer species. The action of termites and cerambycid larvae may facilitate decay entry and spread within the stem.

Associations were found between obligate beetle species and rotten wood types. For some obligate beetle species these associations were consistent between trees and log. It is suggested that some beetle species remain within the stem of the tree as it

passes through successional stages, from an old standing tree to a large downed log. This has important implications for the forest industry, as it highlights the potential vulnerability of these species to habitat loss, due to their reliance on a habitat that is only found within older, larger diameter wood and due to their suspected poor dispersal ability.

APPENDIX 6.1.

Detailed descriptions of the rotten wood types categorised from the rotten wood of living *Eucalyptus obliqua* trees in wet eucalypt forest in southern Tasmania.

Discoloured wood

Description taken from Yee (2005), Appendix 4.6.4.

'Discoloured wood comprises any wood that has been slightly discoloured, but still has the apparent physical structure of sound wood. Discolouration can vary from light pink, to yellow, or brown. The wood can have a grainy appearance.'

This discoloured wood type was found in all three living tree age classes in this study.
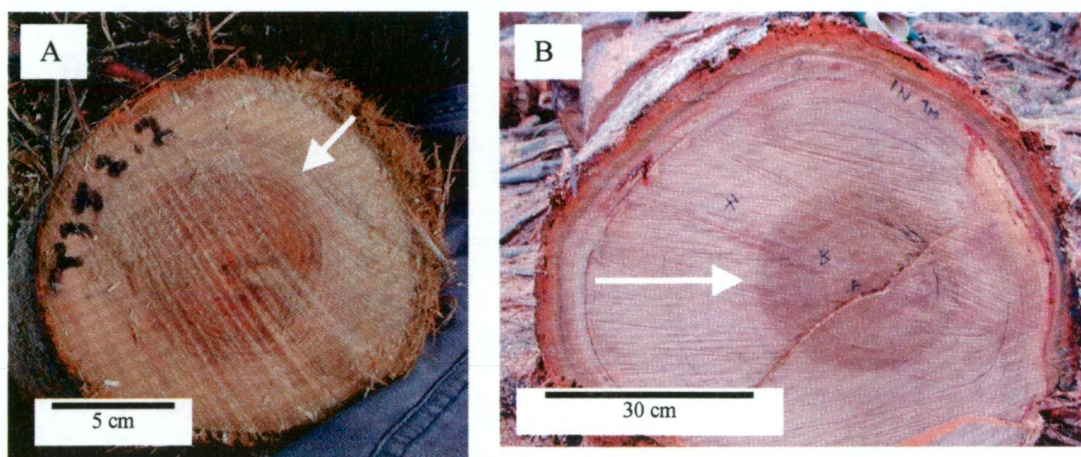
Plate 6.1 Discoloured wood. Arrows indicate edge of discoloured patches in (A) a young tree and, (B) and medium-aged tree.

Termite Damage

Termite damage was characterised by smoothed galleries in both the sapwood and outer heartwood. Frequently termites were found to be still present in these galleries. Termite damage was found in all six of the old study trees and in two of the young study trees.
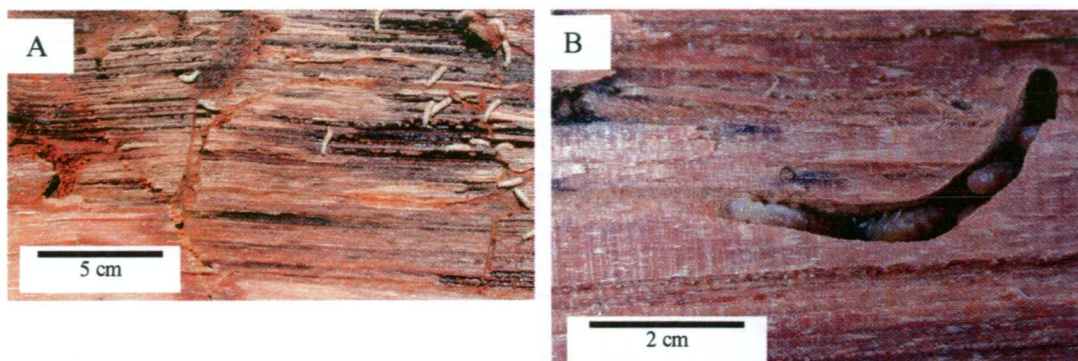
Plate 6.2 Termite Damage, (A) and (B) showing termites and characteristic smooth galleries.

Cerambycid Larva Damage

Cerambycid larva damage is characterised by large stringy frass in both the inner and outer heartwood. Cerambycid larvae were frequently found within this rotten wood type. Cerambycid larva damage was only found in the old trees and occurred in all six (old) study trees.
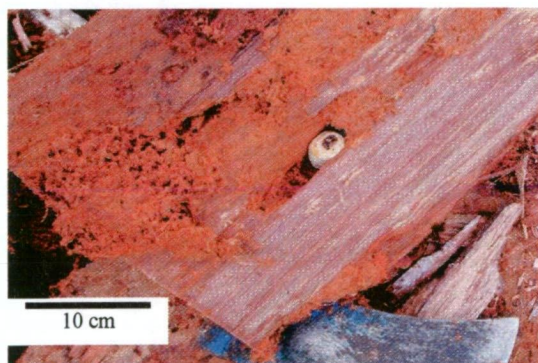
Plate 6.3 Cerambycid larva damage, showing larva and characteristic stringy frass.

Stringy rot

Stringy rot has a coarse stringy texture, with the colour ranging from light brown through to dark reddish-brown. The rotten wood appears to consist of long stringy, wool-like fibres. It differs from the white stringy rot described by Yee (2005) as stringy rot lacks the bleached-white colour and softer, spongy texture of the white stringy rot. This rotten wood type was only found associated with old trees.
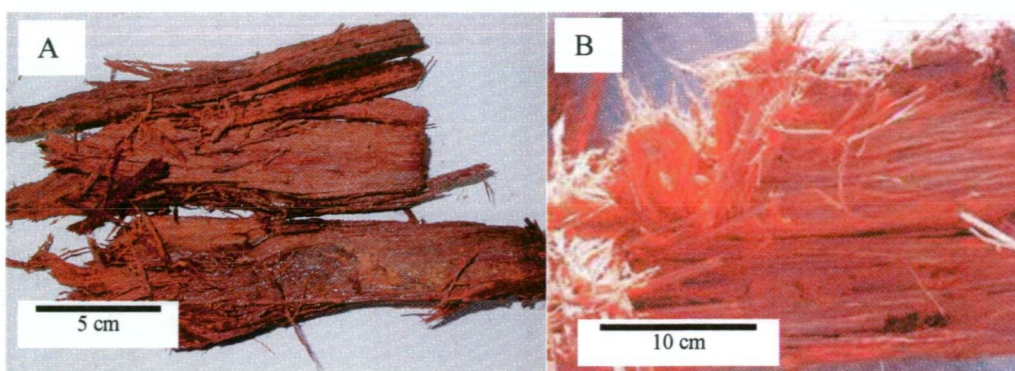
Plate 6.4. Stringy rot, showing colour variation from (A) dark brown through to (B) red-brown. The fibrous texture of this rot is especially evident in (B).

White Spongy Rot

White spongy rot is characterised by continuous long, spongy, wool-like, bleached fibres. The colour can range from white through to a straw-like yellow colour. The rotten wood has a very soft texture and appears to have a very low density, making it very light. This rotten wood type was found in only the two younger age classes: in three young trees and in one medium-aged tree.
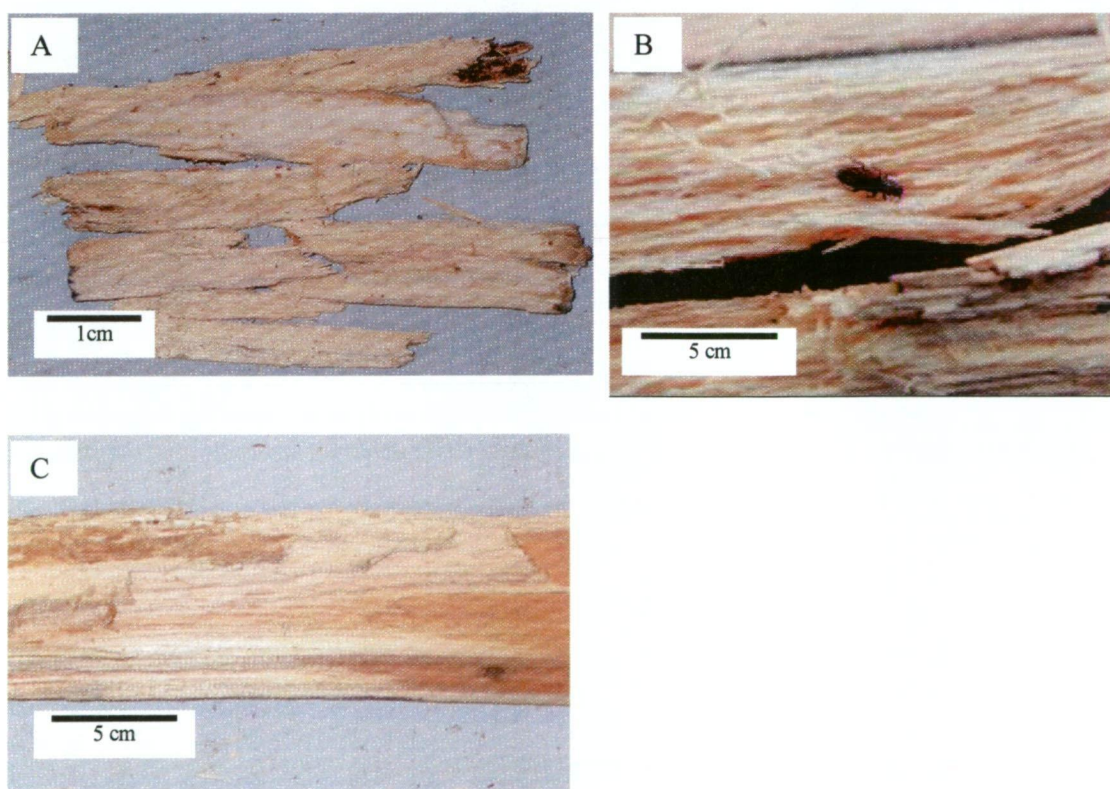
Plate 6.5 White spongy rot showing close-up view of the (A) bleached wood, (B) fibrous wood texture and (C) colour variation from bleached white through to straw-like yellow.

Small Pocket Rot

Small pocket rot is characterised by 2-5 mm elliptical pockets. These pockets are usually empty but are very occasionally filled with white mycelium. Pockets are separated by thin areas of seemingly intact wood. The rotten wood can range in colour from a light tan to dark reddish-brown. This rotten wood type is often associated with black 'zone' lines. It can be distinguished from the white pocket rot described by Yee (2005) as the pockets are smaller (2-5 mm as opposed to 8-20 mm) and are usually dry, rather than filled with gelatinous material or mycelium. It was only found in one living tree in the youngest age class.
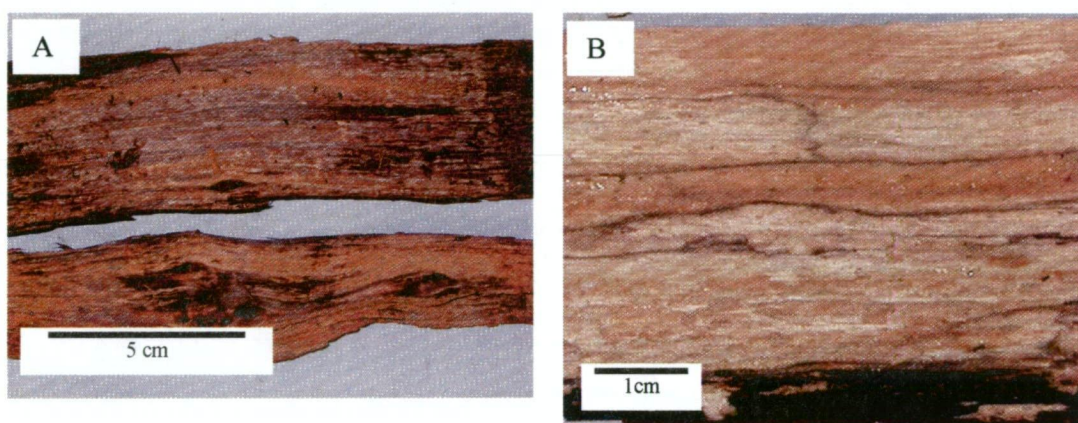
Plate 6.7 Small pocket rot showing small pocket size, empty pockets and colour variation from (A) dark red-brown colour to (B) light tan.

Combination Pocket and Brown Rot

Combination pocket and brown rot appears to be a rot type formed from the action of two different rots: a pocket rot and a brown rot. It is characterised by irregularly spaced 5-20 mm elliptical pockets. These pockets are generally empty but are occasionally filled with white mycelium. In contrast with other pocket rots described, the rotten wood is blocky (i.e. the wood breaks into regular blocks), rather than fibrous, and the wood in between the pockets is soft. The rotten wood is a light brown to red-brown colour. This rotten wood type was only encountered in one old tree.
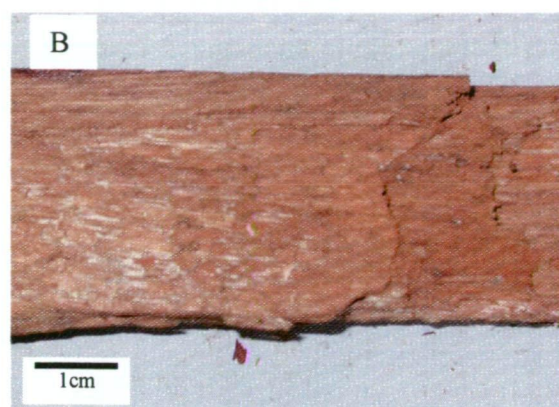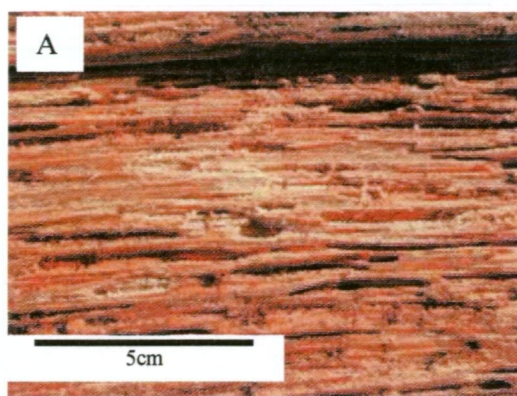
Plate 6.8 Combination pocket and brown rot showing (A) large pockets and (B) blocky nature of the rotten wood.

Dry Brown Cubic Rot

Dry brown cubic rot is characterised by brittle wood that breaks off in regular blocks and can be crumbled by hand to a powder. This rotten wood type ranges in colour from very dry tan to light brown. It is consistently very dry in texture. Distinguishing features include thin sheets of mycelium, with a chamois-like texture, progressing along the rays. This rotten wood type is very similar to the brown cubic rot described by Yee (2005)[1]. Dry brown cubic rot was found in all the old trees examined as well as one of the youngest trees.
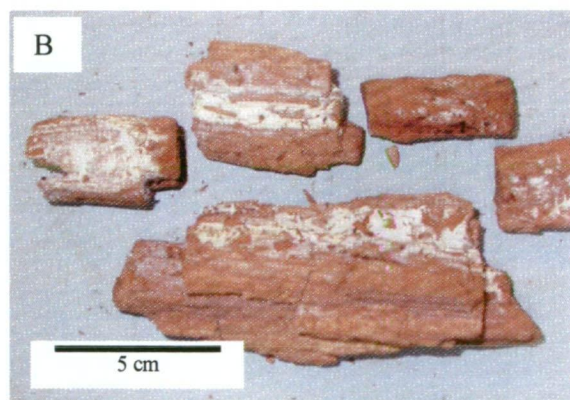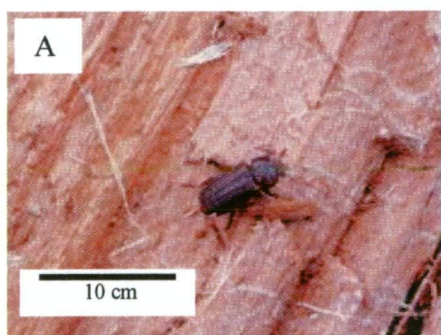
Plate 6.9 Dry brown cubic rot, showing (A) dry, brittle wood and (B) cubic nature of the rot with thin sheets of mycelium.

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[1] Yee's brown cubic rot included both wet and dry cubic rots; however in this study, they were deemed different as they were consistently found to be either wet or dry.

Wet Brown Cubic Rot

Wet brown cubic rot is very similar to dry brown cubic rot except that it is consistently wet in texture. It is characterised by brittle wood that breaks off in regular blocks and can be crumbled by hand to a wet paste. This rotten wood type ranges in colour from red-brown to dark brown. Distinguishing features include thin sheets of mycelium, with a chamois-like texture, progressing along the rays. This rotten wood type is very similar to the brown cubic rot described by Yee (2005)[1]. Wet brown cubic rot was found in all the old trees examined.
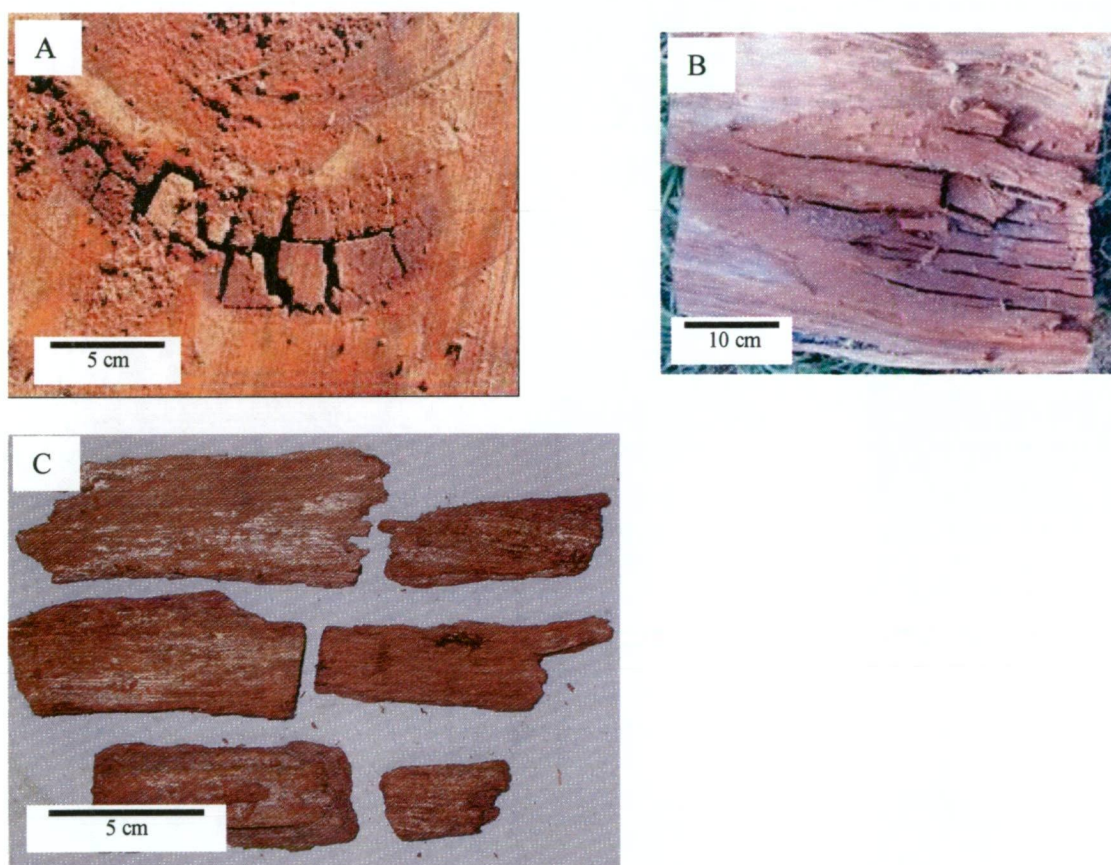
Plate 6.10 Wet brown cubic rot showing (A) cross-sectional view with blocky texture, (B) wet condition of the wood, and (C) dark, wet blocky wood sections with mycelial flecks.

Red-Brown Blocky Fibrous Rot

Description taken from Yee (2005), Appendix 4.6.4.

'Red-brown, blocky, fibrous rot has a distinctive red-brown colour. It is different from brown cubic rot in that it breaks into irregular blocks, and maintains a soft, fibrous, often relatively moist texture, rather than a crumbly, brittle one. In less decomposed wood, the wood is hard, yet the intact wood fibres can be teased apart.

In more decomposed wood, the fibres are more moist and soft, giving the wood a spongy texture. This rotten wood type was mostly found in the central area of the log, but also occurred in localised patches, and occasionally in areas adjacent to the brown blocky crumbly rot.'

In living trees in this study, this rotten wood type was only found in a single old tree.
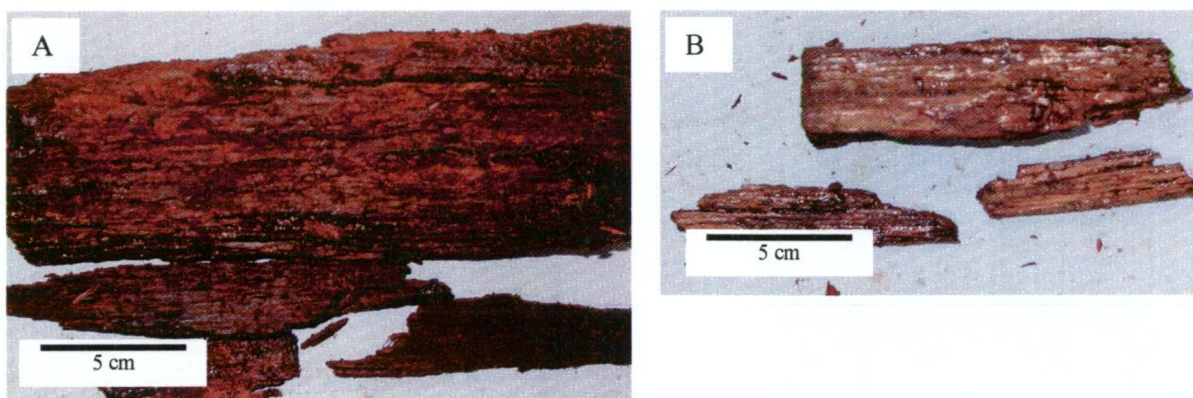
Plate 6.11 Red-brown blocky fibrous rot showing (A) soft, fibrous, moist wood with crumbly texture, and (B) spongy, more advanced rot.

Brown Mudgut Rot

Description taken from Yee (2005), Appendix 4.6.4.

'Brown mudgut rot has a characteristic wet mud- to clay-like consistency, which appears devoid of any recognisable wood fibres. This rotten wood type mainly occurred in the internal heartwood of logs, but was also found in localised patches in the outer heartwood.'

This brown mudgut rot was found only in four old trees.
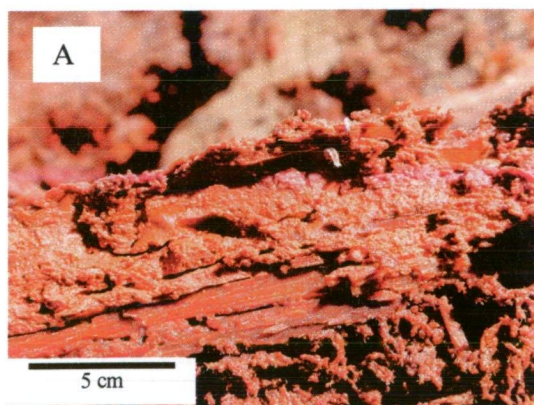
Plate 6.12 Brown mudgut rot, showing typical lack of recognisable wood fibres.

Chapter 7

Study Two

Habitat creation through artificial wounding and burning

7.1 INTRODUCTION

Saproxylic beetles can play an important role as 'ecosystem engineers' by facilitating the creation of more complex habitat features (such as tree hollows) that are utilised by various species including arboreal mammals and birds (Abbott 1998; Gibbons *et al.* 2002; Lindenmayer *et al.* 1991a; Virkkala *et al.* 1994) and a range of invertebrates (Gibbons 1994; Jenkins and Kitching 1990; Jonsell *et al.* 1998; Mackowski 1987; Ranius and Hedin 2001; Ranius and Jansson 2002; Watson and O'Farrell 1991). Saproxylic beetles are often involved in initial colonisation of sapwood exposed by damage to the protective bark (Speight 1989). These primary species can then assist the colonisation and spread of other decomposition organisms such as wood decay fungi and secondary saproxylic beetle species. The action of these decomposer organisms can lead to the formation of important habitats, such as decayed wood within the interior of the stem which are known to be a specialised habitat for many species of invertebrates and wood decay fungi (Chapter 6; Alexander 2002; Bader *et al.* 1995; Grove 2002c; Jonsell *et al.* 1998; Parsons *et al.* 2003), and may eventually lead to tree hollows being formed. Complex habitat features, such as hollows, generally only develop in older trees (Chapter 2 and 6; Amy Koch, *pers comm.*; Lindenmayer *et al.* 1991a). Older trees are likely to become rarer in the production forest, as they are removed at the time of harvest and under the current prescribed rotation length of 80-100 years there is insufficient time for replacements to regrow (Gibbons 1994; Hickey *et al.* 2001). Artificial damage created by techniques such as mechanical wounding or prescribed burning may increase the rate of habitat formation in younger trees (Key and Ball 1993; Adkins 2006).

In Australia there are no primary excavators (such as woodpeckers) of tree hollows, and hollow formation is therefore dependant on natural branch shedding, as well as

on damage to the tree caused by wind, fire, lightning, wood-decay fungi or wood-boring invertebrates (particularly termites) (Adkins 2006; Gibbons 1994; Inions *et al.* 1989; Mackowski 1987; Whitford 2002). These damage events, and agents of damage and decomposition, can facilitate hollow formation, by providing entry into the sapwood and heartwood for other decomposer organisms (Greaves and Florence 1966; McCaw 1983; Perry *et al.* 1985; Wilkes 1982), exposing previously decomposed heartwood (Gibbons *et al.* 2000; Mackowski 1984), and creating large wounds that are difficult for the tree to occlude (Gibbons 1994).

Termites have been found been to be important in the formation of hollows in some eucalypt species such as blackbutt (*Eucalyptus pilularis*) (Mackowski 1984). Mackowski (1984; 1987) found that beetles in the families Lucanidae, Passalidae and Dynastinae were involved in the later stages of hollow formation and contributed to the enlargement of hollows in *Eucalyptus pilularis,* but little is known about the role of other invertebrates in hollow formation in eucalypts. Invertebrates, particularly those capable of wood-boring, are also likely to facilitate hollow formation by providing entry points for other decomposer organisms; enhancing decay spread within the wood by tunnelling and comminution; and acting as vectors of wood-decay fungi (Crowson 1981; Müller *et al.* 2002; Swift and Boddy 1984). Larger wood boring beetle adults and their larvae such as the larvae of Cerambycidae species can be responsible for the comminution of substantial areas of wood (*pers. obs.*; Käärik 1974), and their role in hollow formation may be akin to that of termites.

The presence of hollows has been linked to tree age, with eucalypt species generally starting to form hollows from 120 to 180 years old (Gibbons 1994; Gibbons and Lindenmayer 1996; Lindenmayer *et al.* 1991a). Larger hollows, which are essential for some vertebrate fauna, usually only develop after a tree has attained an age in excess of 220 years (Gibbons *et al.* 2002). In Victorian *Eucalyptus obliqua,* hollow formation appears to start when the tree is around 110 years old , with the number of hollows reaching a peak at around 430 years old (Ambrose 1982; Gibbons 1994). In Tasmania *E. obliqua* trees less than 100 years old are unlikely to have hollows, medium-sized hollows (entrance diameter 5-10 cm, depth 10 cm) begin to occur in trees 100-140 years and large hollows (>10 cm entrance and 15cm depth) generally only occur in trees greater than 140 years old (Amy Koch, *pers. comm.*).

The natural rate of hollow formation can be artificially accelerated by a range of tree mutilation techniques, such as using chainsaws to initiate hollow formation; inoculation of heart-rot inducing fungi to create hollow trees; artificial establishment of termites; and even using explosives to shatter boles and branch stumps (see Key and Ball (1993) and Lindenmayer *et al.* (1991b) and the references therein). Fire has also been suggested as a method to accelerate hollow formation in eucalypts (Adkins 2006), as it creates damage by killing the bark and exposing the cambium and sapwood (fire-scars) to colonising organisms (Taylor and Haseler 1993) . Damage from fire may be different from other types of wounding, as it changes the moisture content of the damaged tissues (Ehnström *et al.* 1995); it may increase the susceptibility of the heartwood to decomposition by creating a net movement of chemicals (Adkins 2006); and may break down anti-fungal and anti-termitic properties within the heartwood (Adkins 2006). Inions (1989) suggested that fire can reduce the time for trees to be hollow-bearing by a hundred years. It also has the potential to cause damage to a substantial number of trees. However, fire may also accelerate the rate of tree death and can lead to an overall reduction in hollow-bearing trees, particularly in areas that have been subject to high-intensity wildfires and/or have less fire-resilient eucalypt species (Adkins 2006; Gibbons and Lindenmayer 1996; Jacobs 1955; Lindenmayer *et al.* 1990).

In systems where wildfires are a frequent element of the natural environment, such as the boreal forests of Northern Europe and Canada, some beetle species have become physiologically adapted to the conditions created by fire (Ehnström *et al.* 1995; Gibb *et al.* 2006b; Saint-Germain *et al.* 2004a, 2004b; Wikars 1992, 1997, 2002). Some species have even developed specialised sensory systems to perceive the smoke and/or heat generated from a fire (Ås 1993). Beetle species have been found to be favoured by fire (fire-favoured), while others appear to be fire-adapted and dependent on fire disturbance (pyrophilous) (Wikars 1992). Fire-favoured and pyrophilous species may be responding directly or indirectly to more favourable conditions resulting from fire, such as an increase in coarse woody debris; a warmer, more sun-exposed and open microclimate; and a reduction in competition (Holliday 1991; Wikars 1992, 1997, 2002). They may also be using the burnt wood as a specific habitat or substrate (Danks and Foottit 1989; Wikars 2002). In Sweden

20 species of beetles are known to be pyrophilous and many more are favoured by fire (Bohman 2004).

Fire is a major natural disturbance factor in the wet forests of Tasmania (Alcorn *et al.* 2001; Hickey *et al.* 1998). Relatively frequent wildfires in parts of the southern wet forests have lead to the development of multi-aged stands, with many trees bearing fire-scars (Hickey *et al.* 1998). At least four wildfires were thought to have occurred in the study region in the 200 yrs from 1600-1800 and four to five wildfires after European settlement (Alcorn *et al.* 2001). As well as fire having a potentially important role in habitat formation in this region, it is likely that some beetle species may have evolved to be adapted to fire disturbance, although this remains unexplored.

This chapter details a manipulative experiment investigating the early colonisation by beetles of fire-damaged or mechanically wounded *E. obliqua* trees, with a focus on the potential of the colonising beetle species for further habitat creation within the tree. It also explores the effect that damage type (wounding or burning) has on the composition of the colonising assemblage. This will assist in developing an understanding of the role that fire plays as a precursor to colonisation in *E. obliqua* and its influence on the species colonising. It may also identify beetle species that favour a burnt substrate.

7.2 METHODS

Data Collection

For full details of the study site and sampling methods see Chapter 2. In summary, forty-five *E. obliqua* trees were chosen and randomly assigned a treatment (fifteen trees from each of three treatments: wound, burn and control) from two adjacent plots in southern Tasmania. Trees were either mechanically wounded or wounded and then burnt (herafter referred to as 'wound' or 'burn' respectively) on their NE faces at a height of 1.8 m, with a wound size of 20cm wide x 50 cm long. Wounds were created by removing the bark and vascular cambium with a chisel and mallet to expose the sapwood. The sapwood was then further damaged by lightly scoring with a chisel. For burnt trees, the exposed sapwood was additionally burnt using an

LPG gas blowtorch until all the sapwood was blackened (approximately 20 minutes per tree). The bark had to be removed prior to burning as the LPG gas blowtorch used to burn the trees was unable to ignite the thick layer of bark present. The type of damage created by removing the bark prior to burning would be more akin to an intense wildfire that destroys the complete cambium layer.

Capturing beetles 'arriving'

A sticky trap (20cm wide x 60 cm long) was constructed from wire mesh and coated with Tanglefoot®. This was placed half over the lower portion of the wound or burn and half over the bark below the wound or burn to capture beetles 'arriving' at the site of treatment. This left the top half of the wound exposed for invertebrates to colonise. Control trees had a sticky trap of the same dimensions attached to the stem at the same height and orientation as on the damaged trees. Sticky traps were serviced every two weeks for six months: from November 2003 until April 2004. All collected beetles were removed from the traps with forceps, then mounted and identified to morphospecies.

Capturing beetles 'departing'

One year after the artificial damage (wounds and burns) had been created, beetles emerging from these damage treatments were captured using a modified emergence trap. This emergence trap was placed over the top half of each wound or burn (i.e. the portion which had not been previously covered with a sticky trap) and was fitted with a top and bottom collection head. Control trees had an emergence trap fitted at the same height and orientation as on wounded and burnt trees. Beetle emergence was monitored for six months from November 2004 until April 2005, with all beetles collected being mounted and identified to morphospecies.

Several environmental variables were recorded for each tree including diameter at breast height over bark (DBHOB) and the distance into the standing forest from the harvested part of the coupe (measured from the closest edge). See Chapter 2 for details of recorded variables.

Data Analysis

Separate analyses were conducted on beetles captured 'arriving' from those captured 'departing' to assess both beetles' 'attraction to' and 'ability to colonise' a treatment.

Comparing species richness

The mean numbers of saproxylic beetle individuals and species were calculated 'arriving' and 'departing' for each treatment. Any significant difference in means was tested using a one-way analysis of variance (ANOVA) and a follow-up multiple comparison test (Ryan-Einot-Gabriel-Welsch Multiple Range Test: REGW test) in SAS 9.1 (Anon. 2002).

Comparing species composition

The effect of treatment on saproxylic beetle species composition 'arriving' and 'departing' was initially compared using an unconstrained ordination (Non-metric Multidimensional Scaling (NMS)) and Multi-Response Permutation Procedures (MRPP) (see Chapter 2 for further details on these statistical analyses). As some beetle species may be 'responding' to damage regardless of whether the tree was burnt or mechanically wounded, effects of treatment on beetle composition were also investigated by pooling the datasets of the two damage treatments (wounded and burnt) and comparing this to the control. Effects of other measured variables (plot, diameter, distance within aggregate, and the combination of plot and distance within aggregate) on species composition were investigated using the same techniques (i.e. NMS and MRPP). Two categories were defined for distance within standing forest: edge (0-5 m) and interior (>5 m), and three categories for tree DBHOB: < 30 cm, 30-70 cm and > 70 cm.

Additional NMS and MRPP analyses were conducted on a subset of beetles captured 'arriving'. This subset only included beetle species that had been captured 'departing' as well as 'arriving', in an attempt to exclude species whose presence is likely to bear little relation to the treatments (such as the normal stem fauna or 'tourist' species that have inadvertently been captured). Little is known about the

life history of most captured beetle species, making it difficult to be able to identify any species that could be excluded from the analysis to focus more on those that were 'meant' to be sampled. As beetles captured 'departing' are more likely to be associated with the treatments, exclusion of all beetle species not captured departing was considered the best available approach to focus on beetles 'responding' to treatment.

The effect of treatment on saproxylic beetle species composition 'arriving' and 'departing' was also investigated using a constrained ordination technique, canonical analysis of principal coordinates (CAP). This allowed the effect of treatment to be explored more explicity as this analysis explores the differences between *a priori* groups. Separate CAP analyses were conducted to investigate: the effect of each treatment (with three *a priori* groups: wounded, burnt and control); the effect of damage (with two *a priori* groups: combined damage treatments and control) and to separate the effect of each damage treatment (with two *a priori* groups: wounded and burnt).

Specialists of a treatment

Preferences for a particular treatment by species captured 'arriving' and 'departing' were investigated using two methods, Indicator Species Analysis (Dufrêne and Legendre 1997) and correlation analysis based on canonical axes derived from CAP (Anderson and Willis (2003) (see Chapter 2 for further details). Two CAP analyses (as detailed in the above section) were used to determine species 'preferences'. Correlation analysis based on the canonical axes from the CAP, with two *a priori* groups (combined damage treatments and control), allowed identification of species that 'preferred' the damage treatments and those that 'preferred' the control. Species that 'preferred' the wounded treatment or the burnt treatment were determined by correlation analysis based on the canonical axes from the CAP with two *a priori* groups: wounded and burnt. Only species that had been previously found to 'prefer' the damage treatments rather than the control were considered. Significant correlation was defined by $| r | > 0.3$ for each of the canonical axes.

7.3 RESULTS

Description of fauna

In total, 280 species of saproxylic beetles (5880 individuals) were collected. The majority of beetle species and individuals were captured arriving at the study trees rather than departing from them (Figures 7.1 a and b). For arriving beetles, a greater number of species was collected at the burnt treatment than at either the wounded treatment or the control (Figures 7.1 a and b). A different trend was seen for departing beetles, with the control and wounded treatment having the same number of species, each more than the burnt treatment. The wounded treatment had the greatest number of individuals captured departing.
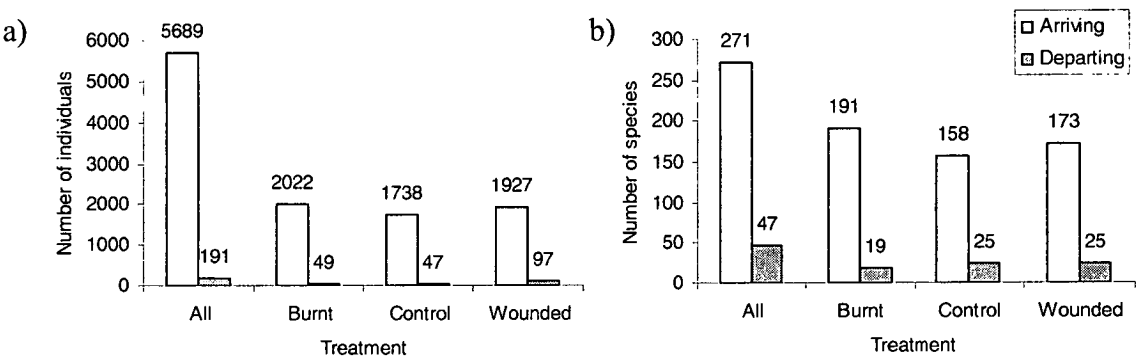
Figure 7.1 Number of saproxylic beetle a) individuals and b) species captured arriving and departing for all treatments combined and for each individual treatment. Note the axes are different scales.
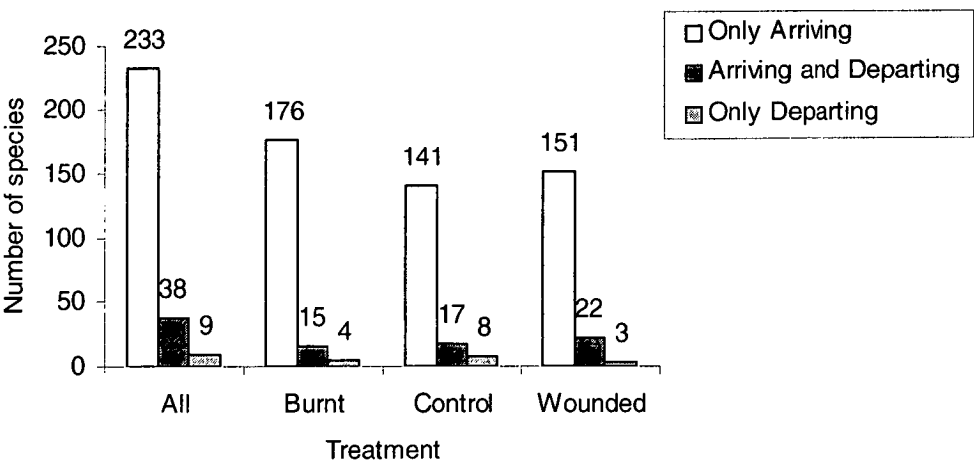
Figure 7.2 Distribution of saproxylic beetle species captured arriving or departing for all treatments combined and for each individual treatment.

A greater number of species was captured only arriving for all treatments (Figure 7.2) with just 38 species collected both arriving and departing from all sampled trees. The wounded trees had the greatest number of species captured both arriving and departing.

Effect of Treatment
Comparison of species richness

Beetles Arriving and Beetles Departing

No significant differences were found in the mean number of either individuals or species by treatment, for beetles captured arriving (Figure 7.3). Wounded trees yielded significantly more individuals and species departing than did burnt or control trees.
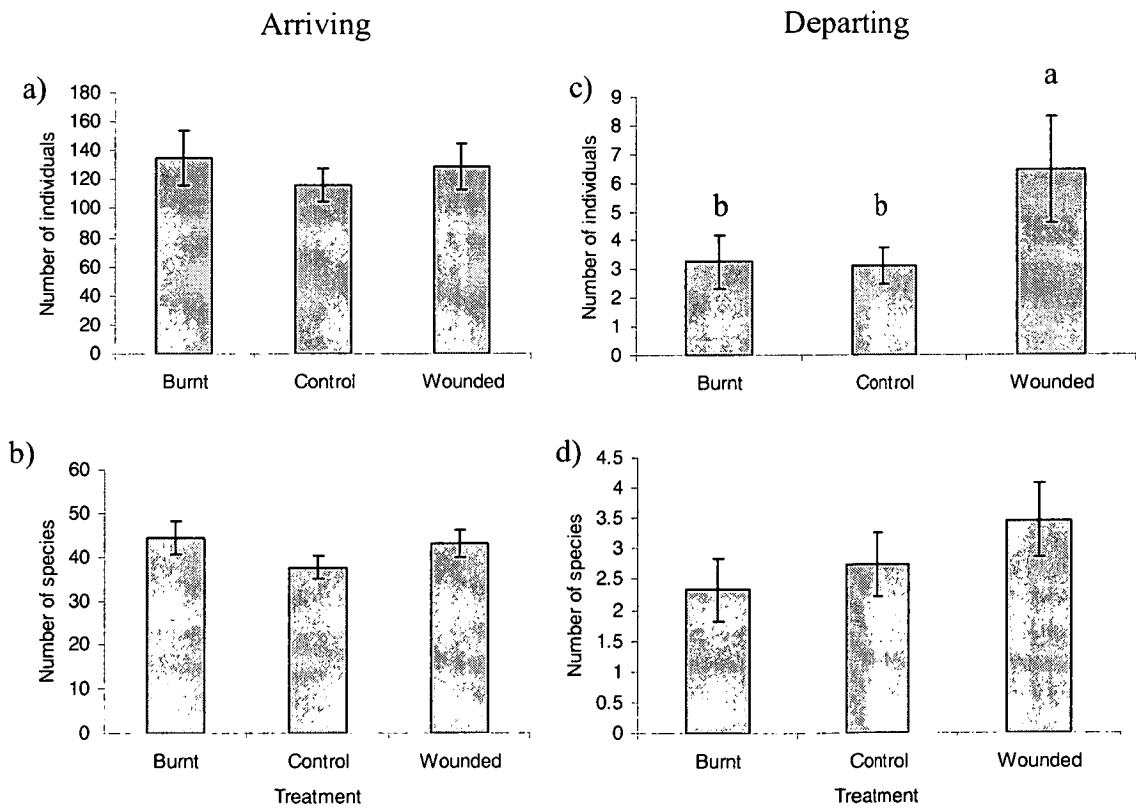
Figure 7.3 Mean number of saproxylic beetle a) individuals and b) species captured arriving per tree for each treatment and mean number of saproxylic beetle c) individuals and d) species captured departing per tree for each treatment. Error bars show standard error. Note the axes are different scales.

Comparison of species composition

Beetles Arriving

The NMS ordination of the assemblage composition of beetles (captured) arriving showed some separation between the damaged and control trees (Figures 7.4 a and b). No clear separation was seen between the two damage treatments (Figure 7.4a). No significant difference was found using MRPP between the beetle assemblages arriving at either of the damage treatments (burnt or wounded) and the control; nor between beetles assemblages arriving at the combined damage treatments and the control (Table 7.1).
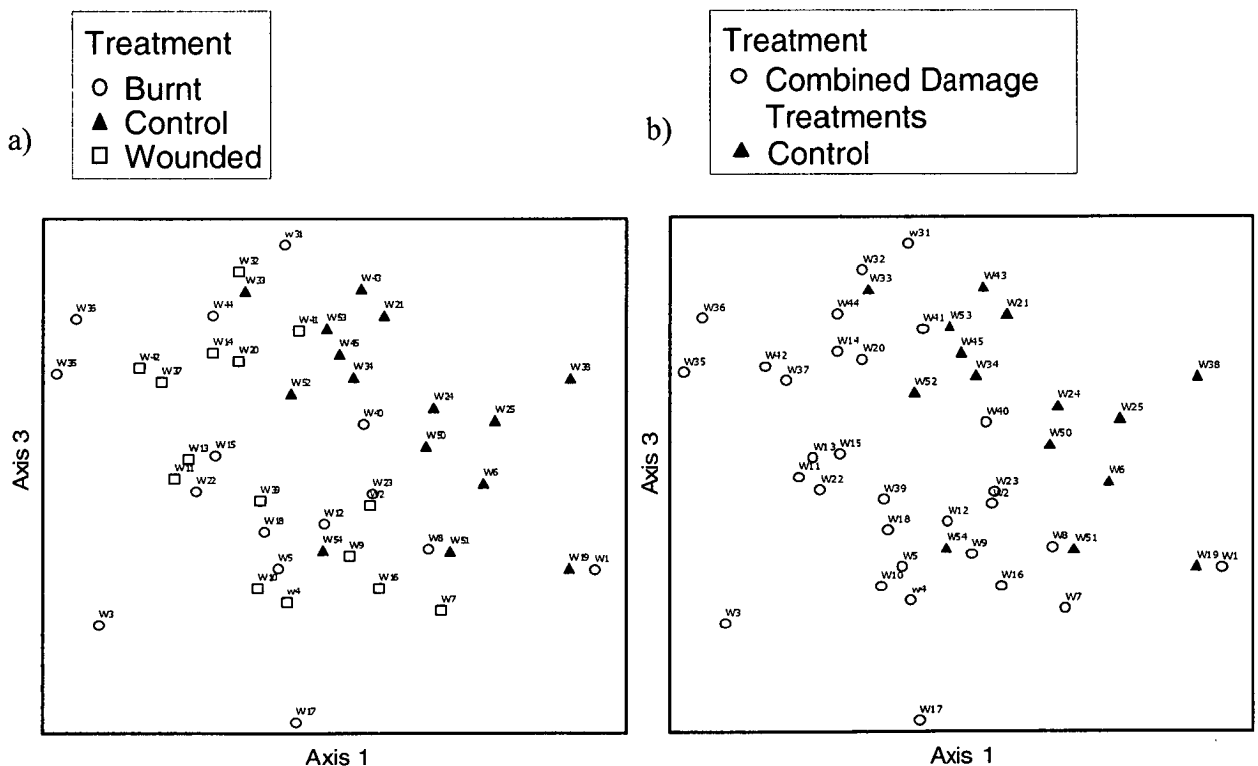
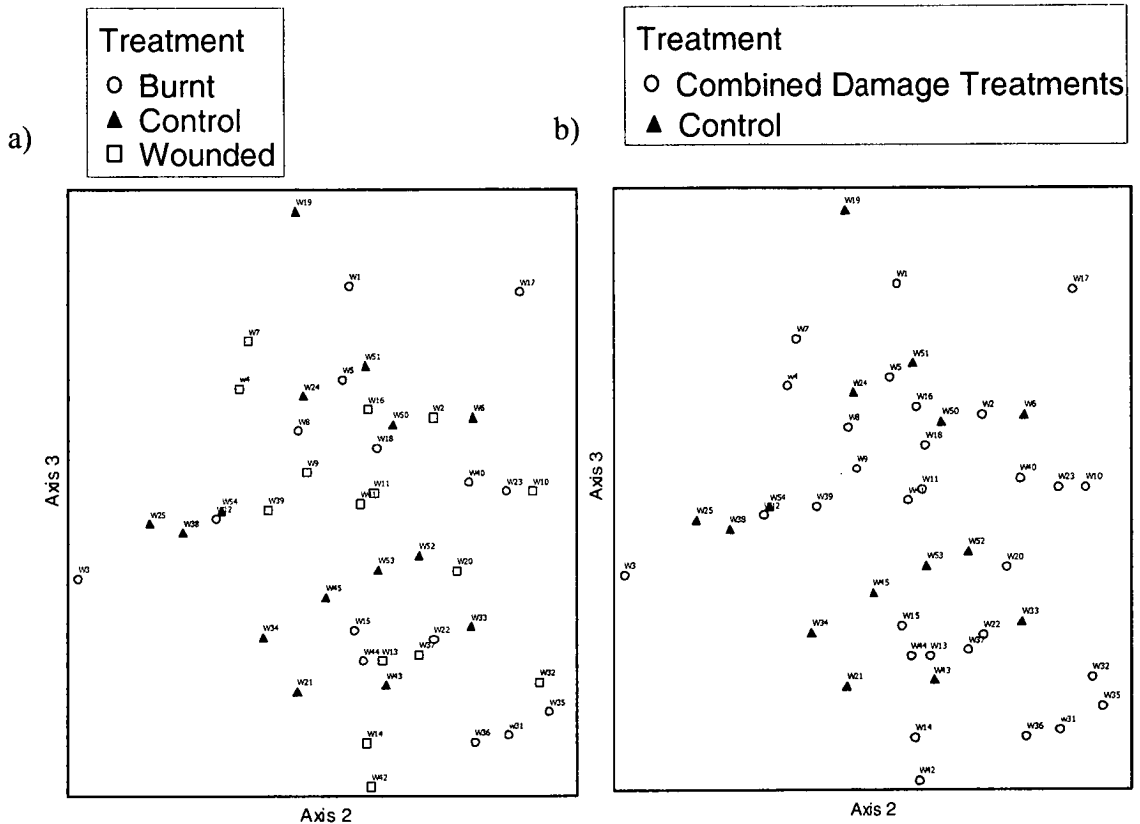*Figure 7.4 NMS ordination of saproxylic beetles captured arriving at all sample trees showing a) each treatment and b) combined damage treatments and control. Axes 1 and 3 from a total of three axes are shown. Abundance data were log_{10} (x+1) transformed and singletons excluded. Stress = 18.01*

Table 7.1 MRPP p-value results testing null hypotheses of no difference in saproxylic beetle composition (captured) arriving for each treatment, for each plot, for each distance within aggregate, and for distance within each aggregate for each plot. Significant differences are marked with a *.

Comparison Categories	MRPP p-value
Treatment	
Burnt vs Wounded	0.968
Burnt vs Control	0.365
Wounded vs Control	0.300
Combined Damage Treatments vs Control	0.220
Plot	
Plot 1 vs Plot 2	*0.000004**
Distance within aggregate	
Edge vs Interior	*0.00006**
Plot and distance within aggregate	
Plot 1 Edge vs Plot 1 Interior	*0.0058**
Plot 2 Edge vs Plot 2 Interior	*0.0064**
Plot 1 Edge vs Plot 2 Edge	*0.00003**
Plot 1 Interior vs Plot 2 Interior	*0.0499**
Diameter Class*	
< 30 cm vs 30-70 cm	0.118
< 30 cm vs > 70 cm	0.230

A closer investigation of the results shows several factors to be contributing to the variation in assemblage composition (Figures 7.5 a-c, Table 7.1). Using symbols that distinguish between the two plots allows recognition of a clear effect of plot on the ordination (Figure 7.5a). A similar pattern is seen for the distance the sampled tree was within the aggregate, with a high degree of separation between the interior and edge trees (Figure 7.5b). Some separation can also be seen for the distance the sample tree was within the aggregate at each plot (Figure 7.5c). No separation could be seen between the diameter classes (Figure 7.5d). MRPP analysis supports these findings with a significant difference in assemblage composition of saproxylic beetles captured arriving at each plot; at the interior versus the edge; at the interior versus the edge of each plot; and at the edges versus the interiors of the two plots (Table 7.1). No significant difference was found using MRPP analysis for diameter class. It is important to note that the number of trees sampled in each category (other than treatment) is not equal, as the experiment was not designed to investigate these factors.
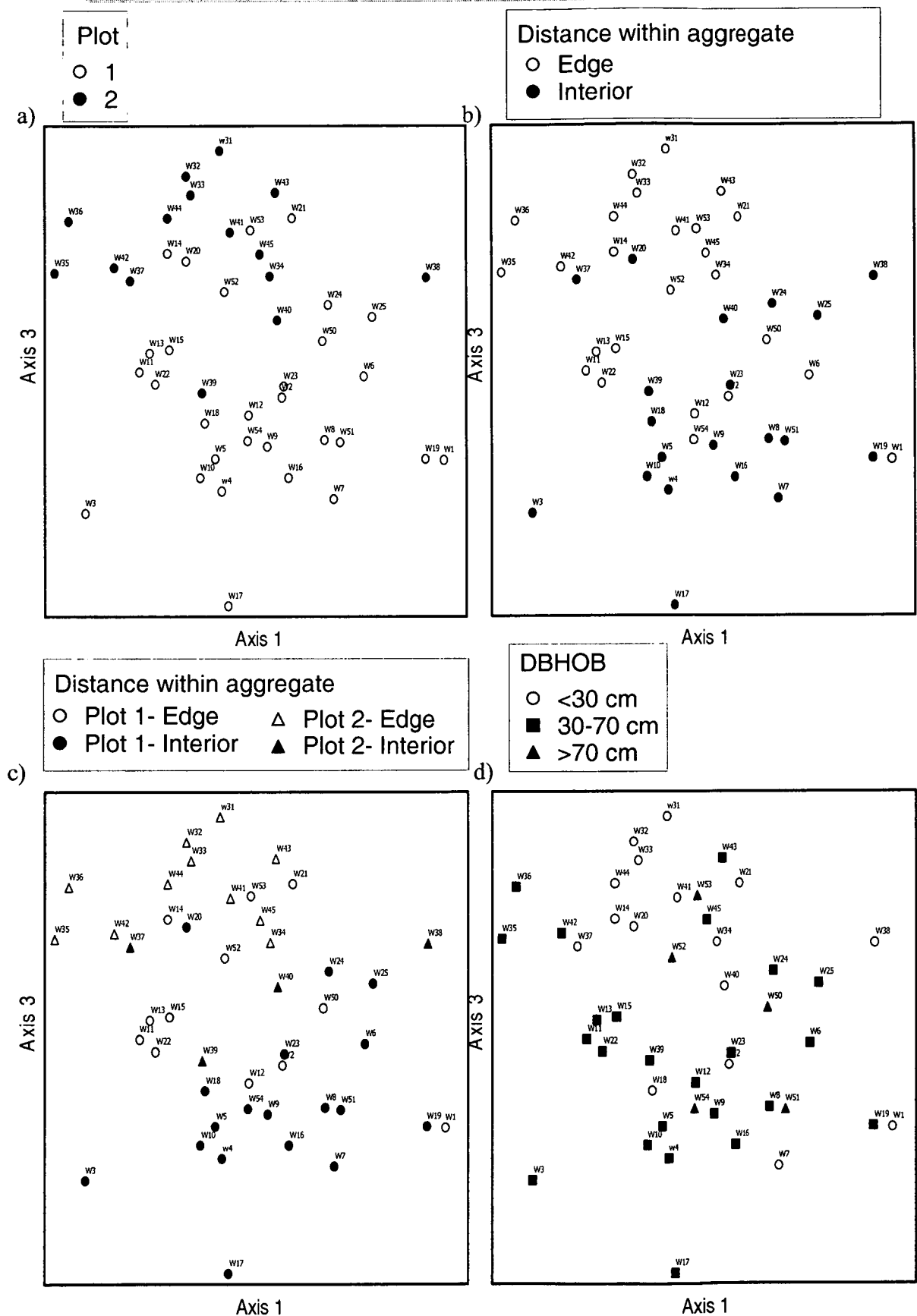
Figure 7.5 NMS ordinations of saproxylic beetles captured arriving at all sample trees showing a) plot, b) distance within aggregate, c) distance within each aggregate per plot and d) diameter (DBHOB). Axes 1 and 3 are shown from a total of three axes. Abundance data were log₁₀ (x+1) transformed and singletons were excluded. Stress = 18.01

The effect of treatment on beetles arriving was investigated using a dataset which included only species captured arriving that had also been captured departing. This was to reduce the influence of beetle species that are not likely to be 'responding' to the treatment, but are either the normal stem fauna or 'tourist' species that have inadvertently been captured. It was felt that these species may be limiting the ability of the NMS ordination and MRPP analysis to determine differences in assemblage composition due to treatment.

Figure 7.6 NMS ordination of saproxylic beetles found arriving that had also been captured departing showing a) each treatment and b) combined damage treatments and control. Axes 2 and 3 from a total of three axes are shown. Abundance data were log₁₀ (x+1) transformed and singletons excluded. Stress = 17.92

No clear separation was found among treatments for this dataset, using NMS ordination (Figures 7.6 a and b). In fact, there was less apparent separation between the damage treatments and the control when using this dataset than when using the complete arrival dataset (Figure 7.4 a and b), suggesting that this approach of selectively excluding species was removing species that had been responding to treatment.

As several factors were found to be significantly affecting the beetle assemblages captured arriving at the sample trees (Table 7.1), a constrained ordination (CAP) was used to investigate only differences in assemblage composition associated with treatment. A clear separation could be seen between the wounded treatment versus the control, the burnt treatment versus the control (Figure 7.7a), and the combined damage treatments versus the control (Figure 7.7b). A permutation test found these differences in assemblage composition to be significant (Table 7.2). Some separation was seen between the two damage treatments (Figure 7.7a). However, when these two damage treatments were investigated in a separate CAP analysis which excluded the control, no significant difference was found (Figure 7.7c, Table 7.2).

Table 7.2 Results of the CAP analyses for beetles captured arriving, examining the effect of treatment. Allocation success is the percentage of trees correctly allocated into each group, δ^2 is squared canonical correlation.

CAP Analysis	Allocation success %			δ^2	p
	Group 1	Group 2	Group 3		
All	46.67 (Burnt)	86.67 (Control)	46.67 (Wounded)	0.95	0.002*
Combined Damage Treatments and Control	90.00 (Combined)	80.00 (Control)		0.72	0.0001*
Burnt and Wounded	53.33 (Burnt)	53.33 (Wounded)		0.72	0.15
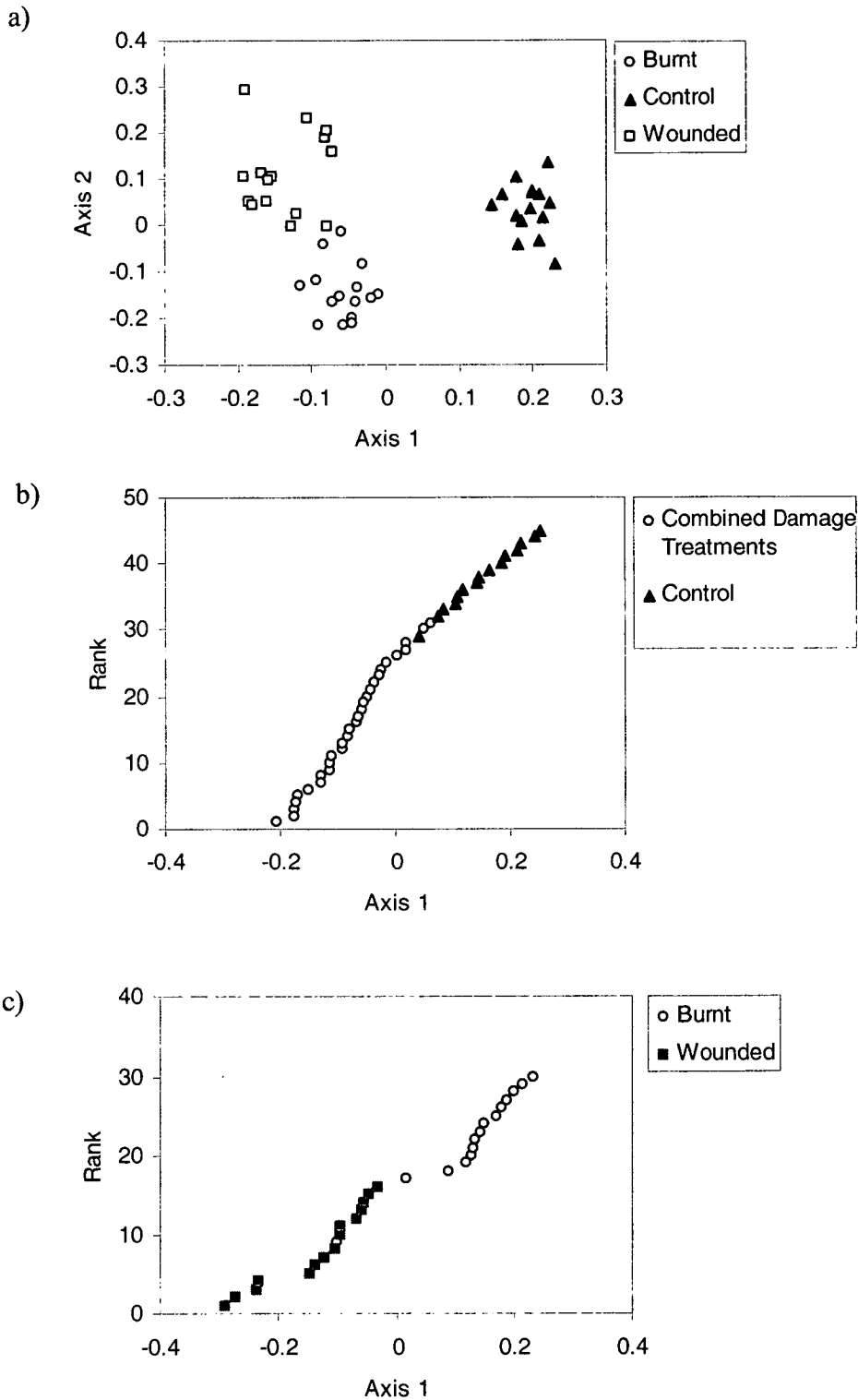
Figure 7.7 Scatterplots of the constrained ordination of beetles captured arriving a) for each treatment (showing the canonical axes 1 and 2 from the 2-dimensional solution); b) for the combined damage treatments and the control and c) for the burnt and wounded treatments (showing axis 1 and rank from the 1-dimensional solution). Data were log(x+1) transformed and singletons excluded.

Beetles Departing

The NMS ordination of beetles captured departing showed a high degree of
separation between the damaged and control treatments (Figures 7.8 a and b)
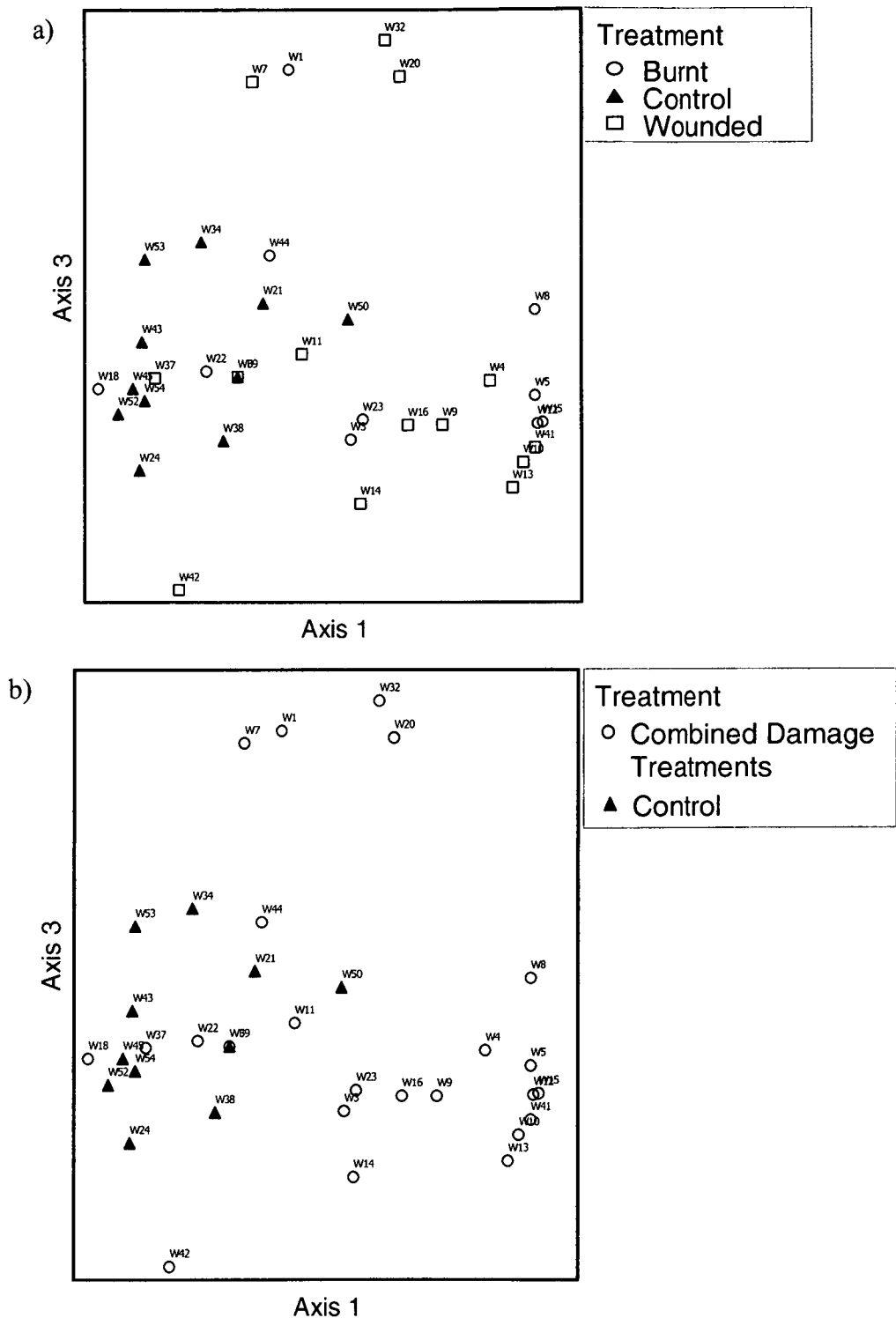
*Figure 7.8 NMS ordination of saproxylic beetles captured departing from all
sample trees showing a) each treatment and b) combined damage treatments and
control. Axes 1 and 3 from a total of three axes are shown. Abundance data were
log₁₀ (x+1) transformed and singletons excluded. Stress = 15.91*

No clear separation can be seen between the two damage treatments (Figure 7.8a). This was supported by the results of the MRPP analyses which found a significant difference between the beetle assemblages departing from either of the damage treatments (burnt or wounded) and the control; and beetles assemblages departing from the combined damage treatments and the control (Table 7.3). No significant effect of plot or distance within aggregate was found on the assemblage composition of beetles departing from the sample trees using MRPP analysis (Table 7.3). However a significant difference in beetle composition was found due to tree diameter (Table 7.3). A high degree of separation between the diameter classes can be seen in an additional NMS ordination (Figure 7.9).
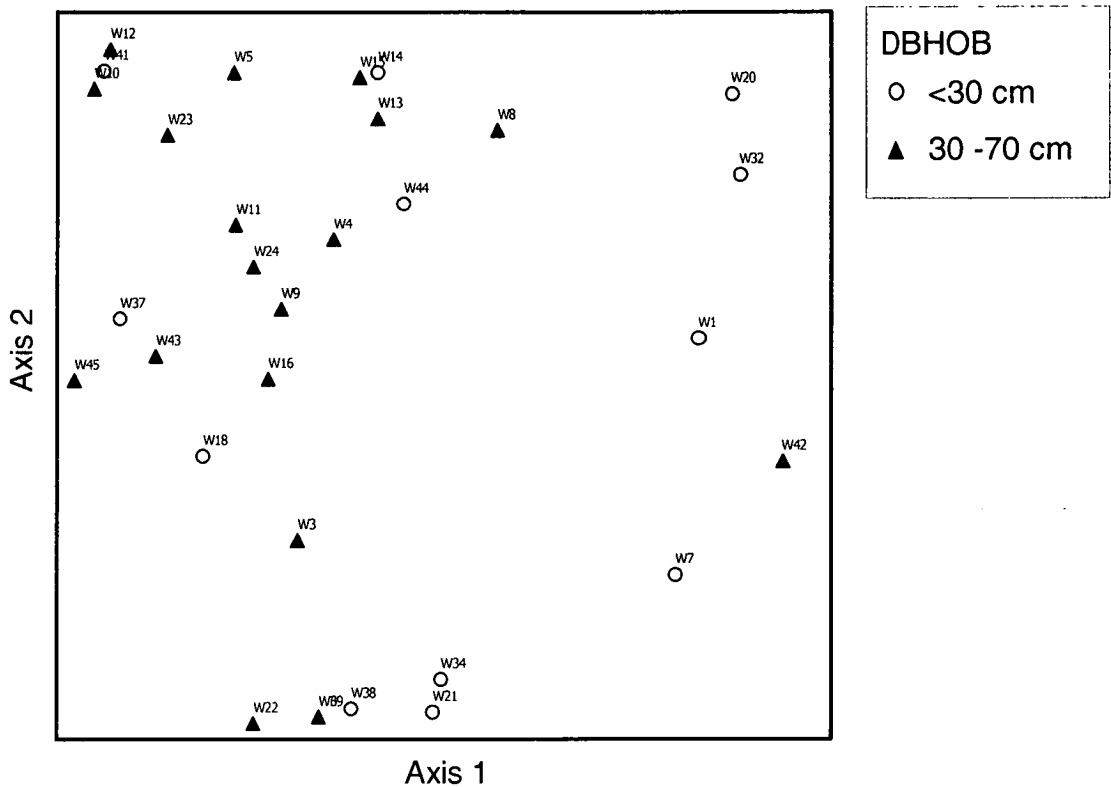
Figure 7.9 NMS ordination of saproxylic beetles captured departing showing tree diameter. Axes 1 and 3 from a total of three axes are shown. Abundance data were $log_{10}(x+1)$ transformed and singletons excluded. The > 70cm class was excluded from the analysis as it only contained control trees. Stress = 16.64

*Table 7.3 MRPP p-value results testing null hypothesis of no difference in saproxylic beetle composition (captured) departing for each treatment, for each plot, and for each distance within aggregate. Significant differences are marked with a *.*

Comparison Categories	MRPP p-value
Treatment	
Burnt vs Wounded	0.59
Burnt vs Control	0.005*
Wounded vs Control	0.009*
Combined damage treatments vs Control	0.0038*
Plot	
Plot 1 vs Plot 2	0.15
Distance within aggregate	
Edge vs Interior	0.39
Diameter	
<30cm vs 30-70cm	0.019*

A similar effect of treatment on the assemblage composition of beetles departing was found using constrained ordination (CAP analysis) and associated permutation test, with a significant difference found between the wounded treatment and the control; the burnt treatment and the control; and the combined damage treatments and the control (Figure 7.10 a and b, Table 7.4). Some separation was seen between the damage treatments (Figure 7.10a). This was investigated using a separate CAP analysis which excluded the control (Figure 7.10c). However, no significant difference was found between the assemblage composition of beetles departing the wounded and burnt treatments (Table 7.4).

Table 7.4 Results of the CAP analyses for beetles departing, examining the effect of treatment. Allocation success is the percentage of trees correctly allocated into each group, δ^2 is squared canonical correlation.

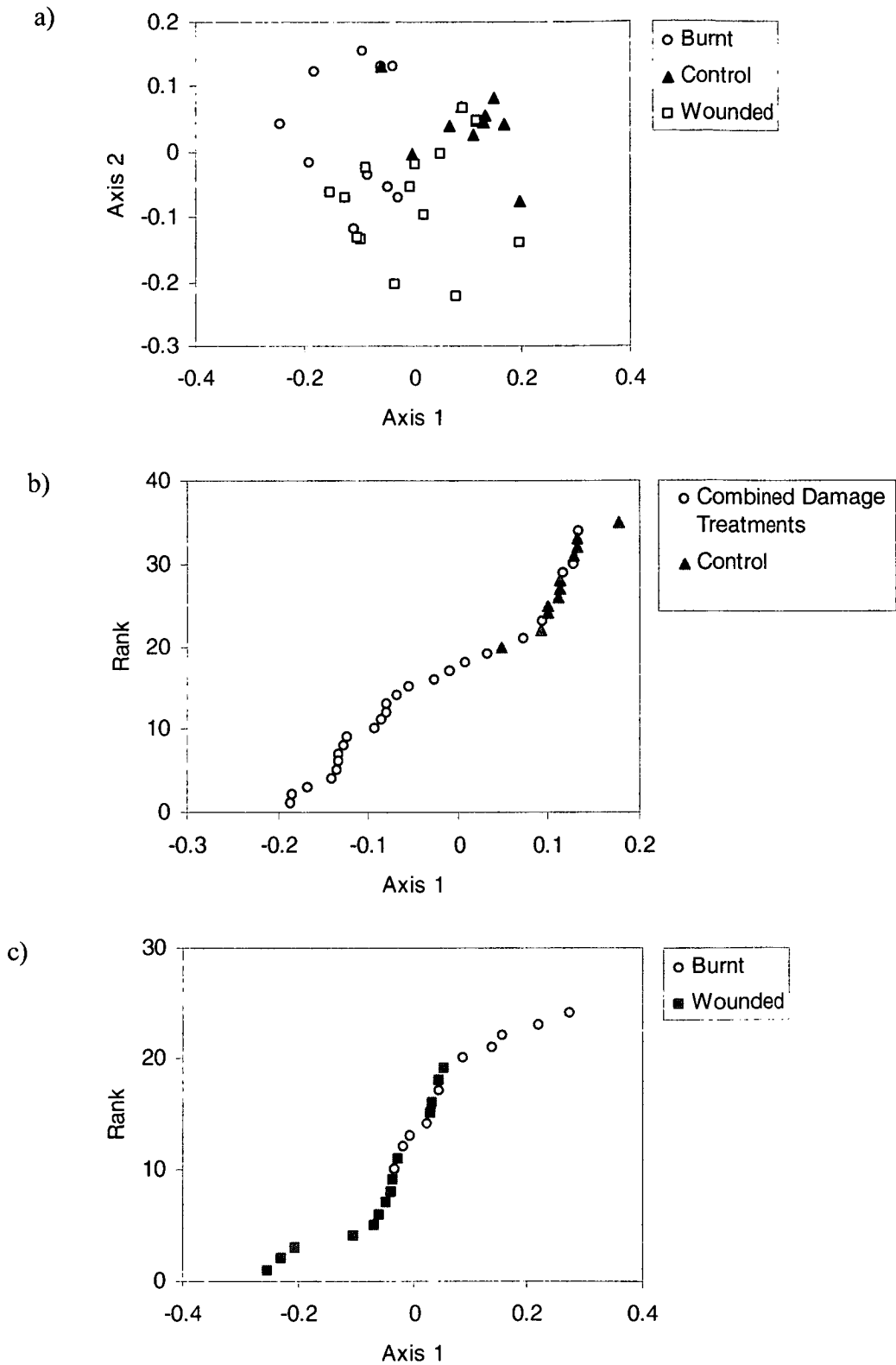| CAP Analysis	Allocation success %			δ^2	p
	Group 1	Group 2	Group 3		
All	25.00 (Burnt)	83.33 (Control)	42.86 (Wounded)	0.5	0.05*
Combined Damage Treatments and Control	79.17 (Combined)	100.0 (Control)		0.45	0.001*
Burnt and Wounded	40.00 (Burnt)	42.90 (Wounded)		0.37	0.29

a)

b)

c)

Figure 7.10 Scatterplots of the constrained ordination of beetles captured departing a) for each treatment (showing the canonical axes 1 and 2 from the 2-dimensional solution); b) for the combined damage treatments and the control and c) for the burnt and wounded treatments (showing axis 1 and rank from the 1-dimensional solution). Data were log (x+1) transformed and singletons excluded.

Specialists of a particular treatment
Arrivals and Departures

Interpretation of species preference by correlation analysis based on canonical axes from the CAP analysis requires a clear difference between the treatments.

Table 7.5 Results of the correlation analysis based on canonical axis derived from CAP (preference defined by | r | > 0.3) and Indicator Species Analysis (preference defined by p <0.05) for the effect of treatment.

Family	Species	Arrivals			Departures		
		Correlation with canonical axis	Ind Val	*p*-value	Correlation with canonical axis	IndVal	*p*-value
Species that 'preferred' the burnt treatment							
Laemophloeidae	*Laemophloeidae* TFIC sp 03	-0.2953	35.6	0.006	-0.297	25.5	0.045
Anobiidae	*Ptinus exulans*		38.1	0.008			
Staphylinidae	Aleocharinae TFIC sp 14	-0.4904	46.1	0.026			
Scarabaeidae	*Saprus griffithi*		26.7	0.026			
Staphylinidae	Aleocharinae TFIC sp 13		33.6	0.031			
Curculionidae	*Cossonus* KH sp 01	-0.3937			-0.5626	38.5	0.027
Nitidulidae	*Cryptarcha laevigata*	-0.3355					
Species that 'preferred' the wounded treatment							
Zopheridae	*Pycnomerus* TFIC sp 02	-0.4355	42.6	0.05			
Species that 'preferred' the damage treatments							
Corylophidae	*Sericoderus* TFIC sp 06				-0.5887		
Curculionidae	*Cossonus simsoni*				-0.4542		
Elateridae	*Toorongus jugulatus*				-0.3292		
Carabidae	*Adelotopus dubius dubius*	-0.3087					
Elateridae	*Agrypninae* TFIC sp 01	-0.3558					
Nitidulidae	*Brachypeplus planus*	-0.4133					
Chrysomelidae	*Cryptocephalinae* TFIC sp 02	-0.3920					
Cryptophagidae	*Cryptophagus gibbipennis*	-0.3542					
Anobiidae	*Dryophilodes* KH sp 01	-0.4382					
Nitidulidae	*Epuraea victoriensis*	-0.4213					
Phloeostichidae	*Myrabolia grouvelliana*	-0.2991					
Leiodidae	*Nargomorphus* TFIC sp 02	-0.4003					
Curculionidae	*Platypus subgranosus*	-0.4880					
Nitidulidae	*Thalycrodes pulchrum*	-0.3487					
Species that 'preferred' the control							
Phalacridae	Phalacridae KH sp 01	0.3389	26.7	0.03			
Anthicidae	Anthicidae TFIC sp 01		29.2	0.034			
Scraptiidae	*Scraptia laticollis*				0.3348		
Throscidae	*Aulonothroscus elongatus*				0.4010		
Anobiidae	*Ptinus exulans*				0.4571		
Oedemeridae	*Asclera sublineata*	0.3051					
Nitidulidae	*Cryptarcha australis*	0.3228					
Coccinellidae	*Rhyzobius* TFIC sp 18	0.3506					
Scirtidae	Scirtidae KH sp 01	0.3541					
Scirtidae	Scirtidae TFIC sp 08	0.3612					

As no clear difference was found for the wounded and burnt treatments for the assemblage composition of beetles arriving (Figure 7.7a), nor for all three treatments for assemblage composition of beetles departing (Figure 7.10b), further CAP analyses were conducted to test for species preferences.

Two separate CAP (analyses) were made for each dataset (arrivals and departures): the first involved pooling the two treatments 'wounded' and 'burnt' and comparing this with the control to separate treatment and control effects (Figures 7.7b and 7.10b); and the second was a direct comparison of the wounded and burnt treatments (by excluding the control from the analysis) (Figures 7.7c and 7.10c). Using this approach and Indicator Species Analysis, different species were found to have different treatment associations (Table 7.5).

7.4 DISCUSSION

Summary of the effect of treatment

While there was little variation in the beetle total abundance or species richness between the damage treatments and control, differences were found in the species composition of saproxylic beetles arriving at and departing from the damage treatments and the control. Some separation could be seen in the unconstrained ordination (NMS), suggesting a different composition of beetles arriving at the damage treatments versus the control. This was not supported by the MRPP result, with no significant difference found in the assemblage composition of beetles arriving at the damage treatments versus the control. A significant difference was found using MRPP for two other measured variables (plot and distance within aggregate). The influence of these variables might be reducing the ability of the MRPP to find differences due to treatment. This idea is supported by the significant effect of treatment when using a constrained analysis (CAP), which focuses on the variation in the species composition directly aligned with the damage treatments versus the control.

The effect of treatment on the assemblage composition of beetles departing was clear in both the unconstrained (NMS) and constrained ordination (CAP). This was supported by MRPP and the permutation test in CAP, which found a significant difference between the damage treatments and the control. The two variables (plot

and distance within aggregate) that were found to be significant factors influencing the composition of beetles arriving were not significant factors for beetles departing. This may explain why a significant effect could be found for treatment using MRPP analyses for beetles departing.

No clear difference in assemblage composition between fire-damaged and mechanically wounded trees was found using unconstrained (NMS) or constrained ordination (CAP), nor using MRPP and CAP permutation tests. However, individual species showed preferences for either fire-damaged or mechanically wounded trees. This is discussed in detail below.

Why does the assemblage composition of beetles change with plot and distance within aggregate?

The change in species composition with tree distance within aggregate may be linked to the degree of openness and amount of sun-exposure. Sun-exposure has been found to be a significant factor influencing saproxylic beetle species richness and assemblage composition, with a distinct difference found for sun-exposed versus shaded wood (Gibb *et al.* 2006a; Jonsell *et al.* 2004; Jonsell *et al.* 1998; Kaila *et al.* 1997; Lindhe and Lindelöw 2004; Lindhe *et al.* 2005; Sverdrup-Thygeson and Ims 2002). An increase in forest openness and hence the degree of sun-exposure can be caused by logging, wildfires, windstorms, and insect and disease outbreaks (Kaila *et al.* 1997). Thus the degree of sun-exposure may be one of the factors contributing to the differences in species composition between plots. The second plot was exposed on its northern side (sunniest), and hence would have a warmer microclimate than the first plot that had its sampled edge on the western or southern side. Saproxylic beetle conservation and forest management issues relating to this finding are discussed in Chapter 8.

Why does the assemblage composition of beetles change following damage treatment?

The difference in saproxylic beetle species composition between the artificially damaged trees and the control trees indicates that some beetle species are responding to the damaged treatments. Beetles may prefer damaged wood for a

variety of reasons. Damaged wood may be suitable for beetles that directly feed on the damaged tissue; as suitable sites for oviposition; and as access points into the inner heartwood. Indirect associations, such as feeding on fungi or other invertebrate species that colonise damaged tissue, may also explain beetle preferences for damaged wood (Wikars 2002). Beetle species can detect a damaged host through specific adaptations that allow recognition of volatiles, such as ethanol and various terpenes which are formed when tissue is wounded (Hammond *et al.* 2001; Sullivan *et al.* 2003; Witcosky *et al.* 1987). Beetles may also be attracted by the presence of their own or other beetle species (often through the attraction to pheromones such as aggregation or prey pheromones) (Svensson *et al.* 2004; Weslien and Schroeder 1999) or to fungi that may have colonised the wood (Gibb *et al.* 2006b; Wikars 2002).

In this study four beetle species (*Cossonus* KH sp 01: Curculionidae; *Cossonus simsoni*: Curculionidae; *Platypus subgranosus*: Curculionidae; and *Pycnomerus* TFIC sp 02: Zopheridae) that 'preferred' the damage treatments are xylophagous and are either known as primary colonising species or are likely to be primary colonising species. No xylophagous species was found to 'prefer' the control. The curculionid *Platypus subgranosus,* that was attracted to and colonised damaged trees, is a well-documented wood-boring beetle of many tree species including eucalypt, myrtle and pine (Elliott and de Little 1984). In myrtle (*Nothofagus cunninghamii*), the beetle's tunnels provide entry points for the economically important myrtle wilt fungus (*Chalara australis*) (Kile and Hall 1988). The species appears to be attracted to ethanol from fermenting damaged cells, such as may arise from forest harvesting activities or from naturally falling trees or limbs (Elliott and de Little 1984). Three species (*Cossonus* KH sp 01: Curculionidae; *Cossonus simsoni*: Curculionidae; and *Pycnomerus* TFIC sp 02: Zopheridae) that 'preferred' the damage treatments are also xylophagous and are likely to be primary colonising species. In Study One (Chapter 5 and 6) all were found in solid and decayed wood within the interior of stems of old living *E.obliqua* trees. *Cossonus* KH sp 01 and *Pycnomerus* TFIC sp 02 were also found in young trees, but only in those that had decay (Chapter 6). In studies on recently downed *E. obliqua* logs (Grove and Bashford 2003) and logs of an intermediate decay stage (Yee 2005) within the Warra (study) region, *Cossonus* KH sp 01 was not found and *Pycnomerus* TFIC sp

02 was found preferentially in large diameter logs but only in low numbers (7 and 20 individuals collected from each study respectively). This further supports the theory that these species are involved in the primary colonisation of *E. obliqua* trees. Species in the genus *Cossonus* are known to be able to be wood-boring early colonisers of tree species such as pine (Haack 2006). Another xylophagous cossonine species (*Pentarthrum* TFIC sp 03), which was identified as a potential primary coloniser of *E. obliqua* in the study region in Study One (Chapter 6), was found arriving and departing from damaged trees. This species had a good correlation with the damage treatments (correlation with canonical axes $|r| = 0.28$, which was just under the cut-off significance value of $|r| > 0.3$). Also, in the studies of *E. obliqua* logs by Grove and Bashford (2003) and Yee (2005) *Pentarthrum* TFIC sp 03 has only been collected once from a recently downed large diameter log, which provides additional support for the likelihood that this species has a role in the early colonisation of wounds.

The larval stages of the two elaterid species (*Agrypninae* TFIC sp 01 and *Toorongus jugulatus*) that 'preferred' the damage treatments are thought to be predators of invertebrates that are associated with dead or damaged wood, and the adult beetles may have been attracted to the wounds as sites for oviposition. Many elaterid species have been commonly found as secondary colonisers of dead or damaged wood in other tree species in Northern Europe (Speight 1989). In Tasmania, *Toorongus jugulatus* has been found previously only in old decayed *E. obliqua* trees (*per. obs.*) and its larvae may feed on other invertebrates associated with this habitat. This association may be similar for the predatory staphylinid species *Aleocharine* TFIC sp 13 which has been previously found to be an indicator species for old *E. obliqua* trees (Chapter 5).

Several species that showed a preference for the damage treatments are saprophagous and mycophagous. These beetles may be attracted directly to the damaged tissue or to fungal species that have colonised the wound. Four nitidulid species (*Brachypeplus planus, Cryptarcha laevigata, Epuraea victoriensis and Thalycrodes pulchrum*) were found to prefer the damage treatments. Nitidulid species have been previously associated with newly dead tissue. For example, the nitidulid species *Glischrochilus moratus* is apparently attracted to recently dead

wood via wood volatiles (Lindelöw 1992), where it feeds upon the fermenting sap or fungi from the walls of scolytid beetle galleries (Hammond *et al.* 2001).

Why do some beetles 'prefer' either fire-damaged or mechanically wounded treatments?

Several beetle species were found to have a specific preference for a particular type of tree damage, with seven species 'preferring' the fire-damaged trees and one species 'preferring' the mechanically wounded trees. Although some studies have investigated beetle associations with burnt logs (Wikars 2002) or burnt standing trees (Saint-Germain *et al.* 2004a, 2004b), few studies have directly compared beetle associations with burnt trees versus wounded trees, making comparisons of the findings from this study with others difficult. Species preferences for burnt or unburnt logs have been observed in Sweden (Wikars 2002). These differences have been attributed to changes in wood properties (such as moisture content) during burning that may favour some beetle or fungal species. The initial colonising species will in turn influence secondary species attracted to the tree damage. For example, Wikars (2002) found certain ascomycete fungi were favoured by burning and preferentially colonise burnt wood. Beetle species that feed on these fire-favoured ascomycete fungi therefore have an indirect association with the burnt substrate. This may be a reason why in this study the two mycophagous species (*Laemophloeidae* TFIC sp 03 and *Cryptarcha laevigata*) were found to favour fire-damaged trees over mechanically wounded trees.

The degree to which the technique used to artificially burn the trees simulates 'natural wildfire' is questionable. Due to technical issues, unlike wildfire the bark was removed and the sapwood exposed before burning was carried out. This may simulate intense wildfire which has the capacity to burn and destroy the cambium layer, but will not simulate the damage caused by a less intensive fire. Many of the environmental conditions created by wildfire have also not been recreated by this study; this is discussed in further detail below in relation to the likelihood of fire-favoured species in Tasmanian wet eucalypt forests.

Potential for further habitat formation?

This study has investigated the early attraction to and colonisation of artificially damaged trees. Several xylophagous species were found to not only be attracted to the damage but also to colonise the exposed wood. Other species may have also colonised the wood but may not have been captured due to an insufficient sampling period (the lifecycle of some beetles will be longer than the single year sampled in this study). The extent of further habitat creation (both decomposition within the stem and hollow formation) from these wounds is unknown. It is possible to estimate the potential of the xylophagous species involved in this early colonisation for further habitat creation, by examination the information collected about these species in previous studies of different aged *E. obliqua* trees (Chapter 5 and 6). Three species (*Cossonus* KH sp 01, *Pentarthrum* TFIC sp 03 and *Pycnomerus* TFIC sp 02) were found in the stems of both younger trees with a small amount of early decay and in old trees with extensive advanced decay. In older *E. obliqua* (>150 years) tunnels created by *Cossonus* KH sp 01 were found throughout the inner and outer heartwood (*pers. obs.*). The actual role of these species in the advancement of decomposition within the stem is unknown, but it is likely that their action can facilitate the spread of decay within the stem by creating access routes within the wood for other arthropods and fungi and by altering the wood properties (surface area, moisture and gaseous conditions), and hence making it more favourable for other organisms (Crowson 1981; Müller *et al.* 2002; Swift and Boddy 1984; Zhong and Schowalter 1989). The beetles may also be acting as vectors for non-wood-decay fungi (which may benefit them or other invertebrates as a food source and may assist wood-decay fungi by altering wood properties), or for wood-decay fungi, which may increase the amount of decomposition within the stem (Boddy 2001; Crowson 1981; Swift 1977; Swift and Boddy 1984).

The long-term extent of habitat creation will depend on the tree's ability to occlude the wound and prevent further invertebrate and decay spread throughout the stem. As discussed above, some of the species that have been attracted to and have colonised the wounds have the potential to facilitate decay spread within the stem. However, the tree's defences may be able to prevent this from occurring. It has been suggested that older trees are more susceptible to attack as they have a reduced ability to effectively occlude wounds (Jacobs 1955; Wilkes 1982), and that the level

of inhibitory extractives in the heartwood decreases over time (Adkins 2006 and refs therein). Tree defensive abilities have also been linked to general health and environmental stress (such as water and light availability). The artificially damaged trees in this study were thought to be 69-110 years old and varied between apparently healthy dominant trees and suppressed trees, so their abilities to inhibit further decay spread may be varied. Even if the tree can effectively occlude this wound (and hence prevent it from becoming a hollow), the damage may have provided an entry point into the inner heartwood from which decay can spread. This can create an important habitat for other invertebrate (including beetle) and fungal species within the stem and it has the potential to create a further habitat (hollows) in the future (from events such as natural branch shedding or fire which may expose the rotten inner heartwood). Burnt wood may have a different ability to occlude and defend against decay spread than wounded wood, and the initial damage response appears to be different between treatments (*pers. obs.*). The treatment trees are situated within a silvicultural trial and it may be possible in the future to examine the succession of both invertebrate and fungal species and assess the longer-term effects of the artificial wounding and burning.

Are there any fire-favoured or pyrophilous species?

It is possible that some beetle species in the wet forests of Tasmania have, like their counterparts in other forest systems with a similar fire regime, become 'adapted' to fire disturbance (Saint-Germain *et al.* 2004b; Wikars 2002). This study has only considered species that may be attracted to burnt wood on a living tree as a preferred substrate and has not investigated species that may be responding to other conditions created by a wildfire or that utilise other burnt wood substrates (such as trees killed by wildfire or downed wood burnt by wildfire). An attempt has been made to conduct this study in a site that somewhat replicates some of the environmental conditions created by a wildfire (such as openness and a larger quantity of burnt dead wood) by using plots of trees retained in a recently felled and burnt coupe. This may have increased the likelihood of capturing beetles that favour a combination of a burnt wood substrate and environmental conditions associated with a natural wildfire. In Sweden, fire-favoured and pyrophilous beetles are generally in higher abundances at a wildfire site immediately following the event

and for a period of around five years following (Wikars 1992, 2002). The prescribed burning of the surrounding coupe after felling eight months prior to this study may have attracted fire-associated beetles to the site. This may have increased their chance of being captured on all sticky traps, not only those placed over the burnt wood.

The seven beetle species that have been found to 'prefer' the burnt treatment may be considered to be fire-associated and may be favoured by fire, but further studies would be needed to elucidate this. True pyrophilous (fire-adapted) invertebrates are those (as defined by Wikars (1992)) that are totally dependent on fire disturbance and have their main occurrence in burnt forest 0-5 yrs after fire. Even in countries such as Sweden where beetles and their associations with fire are better known, the classification of a species as pyrophilous is still debated as additional studies question previous assumptions (Bohman 2004; Gibb *et al.* 2006b). The laemophloeid *Laemophloeidae* TFIC sp 03 was found to be only attracted to and to only emerge from burnt wood and a species in the same family (*Laemophloeus muticus)* is known to be pyrophilous in Northern Europe (Wikars 1992), thus making it a strong candidate to be classed as a fire-adapted species. The tendency of the cossonine *Cossonus* KH sp 01 to emerge from burnt wounds may also indicate a strong association with fire; however this species was also found to be attracted to and to emerge from wounds, suggesting it may have a 'preference' for burnt wood rather than a dependence on it.

It is possible that some species may have been captured in too low numbers to observe a substrate preference. For example, a study by Bohman (2004) in Sweden investigated burnt and unburnt sites and collected over 10200 beetles which included over 10 species that were known to be pyrophilous. Some pyrophilous species were clearly more abundant at burnt sites, but for three pyrophilous species, only a few individuals were collected, but exclusively at burnt sites. A species' preference for fire in Tasmanian wet forests may become more apparent in the future, if repeated occurrences are noted in conjunction with a burnt site or burnt substrate. Also there is an indication that for many beetle species, the macrohabitat of recently burnt forest is more important than the burnt wood substrate (Gibb *et al.* 2006b; Wikars 2002). This association was not investigated in this study, so there is

potential for the discovery of many other beetle species that are favoured by environmental changes related to wildfire.

A decrease in the quantity of burnt wood and fire-disturbed habitats as a result of modern forestry practices has been linked with a decline in pyrophilous beetles in Northern Europe, with some species considered threatened and some even locally extinct (Bohman 2004; Ehnström *et al.* 1993; Jonsell *et al.* 1998; Wikars 2002). Prescribed burning of harvested and non-harvested forest has recently been implemented in Sweden and in regions of North America to mitigate the ecological effects of decades of fire suppression (Rowntree 1998). While fire is used in the silvicultural regime in Tasmanian wet forests, it is only used as a regenerative tool after harvesting. This generally confines the burnt substrate to downed wood within an open clearing and while this may resemble some of the habitats remaining after a forest fire (Ås 1993; Baker *et al.* 2004), it does not recreate other habitats, such as fire-scarred living trees and fired-killed standing trees. In addition, other factors such as fire distribution, frequency, severity and intensity are likely to be different in a wildfire compared with the silvicultural felling and regeneration burning (as reviewed in Baker *et al.* (2004).

To date there has been a modest increase in the number of fires at least at the Warra site in the 200 years since European settlement (Alcorn *et al.* 2001). However, if the frequency and extent of forest fires in native (managed or reserved) wet forest are significantly changed in the future (for example a reduction through management strategies to reduced fire or an increase or decrease through climate change) it may be necessary to further assess the relationship between beetle species and fire and the impact that a reduction in suitable habitat created by fire may have. This may include developing a better understanding of the role of fire, not only as providing a burnt substrate and a more open environment but as a damage event (often on a large scale) that may be an important pre-cursor to habitat formation within the tree (such as decomposition within the stem and hollows).

7.5 Summary

This study has investigated the colonisation of wounded and burnt wood by saproxylic beetles in *E. obliqua* in the southern wet forests of lowland Tasmania. It

has found several species to be indicative of the initial colonisation including five xylophagous species, some of which are also typical of the interior of rotten, living trees. These species have the potential to facilitate further habitat formation within the tree, by assisting the spread of other decomposer organisms. The long-term results of the damage treatments will depend on many factors including the tree's defence ability.

Several beetle species were found to favour either wounded or burnt wood. This highlights the possibility that some beetle species in the wet forests of Tasmania have, like their counterparts in other forest systems with a similar natural fire regime, become 'adapted' to fire disturbance. Further studies will be needed to elucidate this. Consideration needs to be given to the role of fire in the landscape, not only for creating substrate suitable for some beetle species but as a pre-cursor for habitat formation.

Chapter 8

Summary of findings and implications for sustainable forest management

8.1 INTRODUCTION

This chapter is a synthesis of the major findings of this thesis and discusses the implications for sustainable management of Tasmanian wet eucalypt forests. Management recommendations are made on the basis of the findings from the studies in this thesis. Throughout the chapter future research directions are highlighted.

8.2 SUMMARY OF FINDINGS

Saproxylic beetles inhabiting different aged living **Eucalyptus obliqua**

- Living *E. obliqua* is associated with a high degree of diversity of saproxylic beetles, with 357 morphospecies collected from 63 trees (Chapter 3).

- *Eucalyptus obliqua* trees and logs generally each support a different fauna, with only a quarter of all saproxylic species collected from three studies found in both substrates (Chapter 3).

- Saproxylic beetle fauna differs in old trees (>150 years old) compared to young and medium-aged trees (Chapter 5), with old trees supporting a:

  - higher overall species richness per tree and per surface area sampled;
  - greater richness of obligate beetle species;
  - different assemblage composition of obligate beetle species.

- Young (69 years old) and medium-aged (105 years old) trees have a similar species richness and assemblage composition (Chapter 5).

Saproxylic beetle habitat associations

- Stem-dwellers (rather than branch or bark–dwellers) account for much of the distinctiveness of the saproxylic beetle fauna of trees in the old age-class (Chapter 5). This is likely to be due to a high complexity of microhabitats within the stems of old trees, i.e. the amount and type of rotten wood.

- The findings from Chapter 6 support this idea, with more rotten wood types and a larger proportion of decay within the stems of old trees compared to the two younger age-classes.

- A strong correlation was found between the assemblage composition of obligately saproxylic beetles and the assemblage composition of rotten wood types present within a tree (Chapter 6).

- Several 'key' stem-dwellering obligately saproxylic species are related to European taxa that are considered vulnerable due habitat loss.

- Specific associations with particular rotten wood types were found for several beetle species (Chapter 6). Some of these associations were consistent for both *E. obliqua* living trees and logs.

- Wood fractions with the same diameter have a similar beetle assemblage composition (for example, branches of old trees and the stems of young trees had a similar assemblage composition) (Chapter 5).

- Saproxylic beetle species showed a preference for burnt (seven species) and unburnt (one species) recently exposed sapwood (Chapter 7).

- Saproxylic beetle assemblage composition was found to vary with tree diameter (Chapter 5 and 7); geographical location (over short distances (Chapter 7); and distance from edge of clearing (Chapter 7).

The role of saproxylic beetles in habitat formation:

- Several species with the potential to act as 'ecosystem engineers' (by facilitating habitat formation) in ageing *E. obliqua* trees were identified through comparing findings from Study One and Study Two (Chapter 7).

8.3 POTENTIAL IMPACTS OF CURRENT CBS SILVICULTURE AND THE ADEQUACY OF THE RESERVE SYSTEM

It has long been recognised that forest management that most closely 'mimics' natural disturbance will have the least impact on the forest ecosystem (Franklin *et al.* 2002). In reality, as one of the main objectives of forestry is to harvest timber from the forest, natural disturbance will never be exactly mimicked. However, it is still possible to adapt management practices to minimise both the immediate and long-term effects of timber harvesting.

Conservation issues regarding saproxylic beetle species inhabiting logs and CBS silviculture have already been raised by Yee (2005), who found beetle assemblages differed between small versus large diameter logs; logging regenerated versus mature forest; and a combination of log diameter and forest type. This current study has highlighted potential impacts on saproxylic beetle species inhabiting living trees (particularly old trees) and CBS silviculture. Under the current CBS silviculture regime all trees are removed from the logged coupe and the maximum potential age of the regenerating trees is 80-100 years. To relate regime to the current study, trees from the two older age-classes (and the diversity associated with this mature habitat) will be removed from the coupe at harvest and will not be regenerated. Even if the rotation length were increased to 105 years (the age of the medium-aged trees from this study), it would not be a sufficient length of time for the trees to develop features (such as hollows) and support the same fauna as the old age-class (> 150 years old) (Chapter 2, 5 and 6). As the old trees ages were indeterminate (150 - 400 years old), it is not possible to determine what rotation length would be needed to develop trees comparable with those studied.

This has important implications for the long-term persistence of saproxylic beetle species within a CBS dominated landscape. Local extinctions are likely to occur from forestry operations and natural disturbance (such as stand-replacing wildfire) when habitat is altered. However, with wildfire disturbance this habitat is likely to re-develop over time and as long as spatial continuity is maintained species will generally be able to re-occupy the recovering disturbed area. Areas subjected to a wildfire will generally retain some structural features (such as burnt trees and logs) which, this research and that of Yee (2005) has shown, can harbour some saproxylic

species and aid in maintaining species within the area. Areas managed under a CBS silviculture regime will retain few structural features at the time of harvest and over successive CBS cycles (at the current rotation length), older trees will not re-develop within the stand, and re-establishment of saproxylic species associated with this habitat will not occur (although some species may be able to persist in logs, at least for the short term). The further impact of this will depend on the geographical distribution of the affected species and distribution throughout the landscape of CBS stands and reserves.

Currently little is known about the geographical distribution of these saproxylic species and hence the spatial arrangement of habitat required to ensure their conservation. Studies from the Warra region indicate a high level of beetle diversity that varies considerably over small spatial scales (Baker *et al.* 2006; Yee 2005). Findings from this study support this with significant differences in beetle assemblage composition found between two plots within the same stand (Chapter 7). This suggests that appropriate habitat (a diverse range of structural elements) needs also to be maintained at small scales (such as the stand level).

The Warra region is located all within one bioregion (Southern Ranges Bioregion), which was defined on the basis of vascular plant communities, from which the current reserve system was established. The adequacy of a reserve system for saproxylic beetles which is based on plant communities has not been established. The reserve system has already been found to be inadequate for some log-dwelling lucanid beetles, which have the majority of their geographical distribution outside of reserves (Meggs and Munks 2003). The high level of saproxylic beetle diversity within the Warra region further emphasises the need to assess the adequacy of the current reserve system, as a large number of saproxylic species may potentially be affected by forest harvesting. Studies comparing the saproxylic fauna of different areas within the bioregion will be needed to assess whether the current reserves system is sufficient. This type of study should consider the current unbalanced arrangement of reserves within the Southern Ranges Bioregion, which has substantiality more forest reserved in the west than in the east. This uneven arrangement of the current reserves may be offset by applying a more sympathetic silvicultural regime (i.e. less intensive) within this region to maintain a better balance between timber harvesting and ecological requirements.

8.4 RECOMMENDATIONS FOR OFF-RESERVE MANAGEMENT FOR SAPROXYLIC BEETLE CONSERVATION

Lindenmayer *et al.* (2006) presents a synthesis of broad management principles and a checklist of strategies to guide forest biodiversity conservation; many of these can be directly applied to the on- and off-reserve management of saproxylic beetle species within the wet forests (and this in turn may also correlate with requirements to conserve other forest-dwelling species). Five guiding principles were identified: the maintenance of connectivity; the maintenance of landscape heterogeneity; the maintenance of stand structural complexity; the maintenance of aquatic ecosystem integrity; and the use of natural disturbance regimes to guide human disturbance regimes. The application of these principles and strategies is discussed below, with adaptations to incorporate specific knowledge of saproxylic beetle requirements. Off-reserve conservation management needs to be considered at two scales: stand and landscape.

Stand-level

At the stand-level, the key elements required for saproxylic beetle conservation are (modified from Lindenmayer *et al.* (2006)) stand structural complexity (e.g. large living trees, dead trees with hollows and large fallen logs); longer rotation times (coupled with structural integrity at harvest); silvicultural system change from high impact to lower impact; and appropriate disturbance management. In practice a combination of these may result from the implementation of one factor, i.e. less intensive silvicultural practices will generally increase stand structural complexity.

Alternative silvicultural methods to replace CBS are currently being trialed in Tasmania's wet eucalypt forests (Hickey *et al.* 1999). Some of these silvicultural methods can fulfil the criteria of retaining structural complexity at harvest, as well as keeping harvest yields, production costs and safety considerations within an acceptable range. One technique is aggregated retention, where approximately 30% of the coupe area is retained in 5-6 individual aggregates of 0.5-1 hectare in area (Hickey *et al.* 2001). These aggregates maintain some structural complexity within the stand, providing habitat for saproxylic species. For these to be effective in reducing the impacts of harvesting the design of the aggregates needs to be

carefully considered. Different aged trees need to be retained in each aggregate to immediately support species that require that habitat and to ensure temporal continuity of trees of various ages (and diameters) as the stand ages. Aggregate size also needs to be considered; research in southern Tasmanian forests by Baker *et al.* (2006) suggests that edge effects for litter beetles can reach up to 10-25 metres. On average, she found beetle assemblages were 95% similar to mature forest in areas greater than 22 m from the disturbed edges. The current study found clear edge effects for saproxylic beetles on living trees (Chapter 7). Positioning the aggregates near the edges of the coupe may increase their effective size and lessen potential edge effects, although it may also create larger areas of the coupe devoid of retained trees.

Although retaining aggregates addresses the key element of maintaining structural complexity at harvest, temporal continuity (rotation length) stills needs to be considered. Under the current prescription the stand will be harvested again after 80-100 years, with the future of the aggregates currently undetermined. It is indicated that they may be retained for a second rotation or harvested and new aggregates formed by retaining a portion of the regenerating 80-100-year-old stand (Hickey *et al.* 2001). For saproxylic beetle conservation within the stand, the first option would need to be taken, as new aggregates formed by retaining 80-100-year-old trees would not be able to support beetle assemblages that require the habitat provided by trees older than this (Chapter 5 and 6). If the aggregates are harvested, retaining some of the felled trees will assist in maintaining habitat within the harvested stand. This habitat may provide a refuge for some beetle species that are associated with both trees and logs (Chapter 3 and 6). It will also provide temporal continuity of large diameter debris within the stand, by replacing those that have been decomposing since the initial logging 80-100 years ago.

Initial felling
(First rotation)　　　　　　Second rotation　　　　　　Third rotation
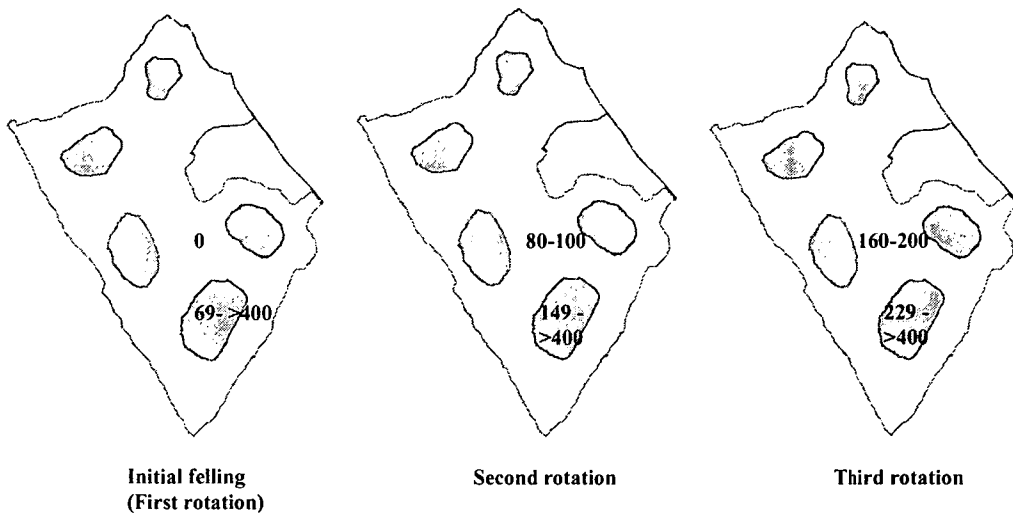
Figure 8.1 Hypothetical age of trees in stand and aggregates after initial felling, second rotation and third rotation based on a rotation length of 80 - 100 years.

If the aggregates are retained, by the beginning of the third rotation the trees in the stand would have attained ages of 160-200 years old (Figure 8.1), and may be suitable for saproxylic beetle species that are associated with older trees (> 150 years old). However, the trees within the stand are not likely to have been subjected to a wildfire, and may not develop the features such as hollows and internal decay that the old trees in this study had until later in their lives. The old trees in this study had been through two documented wildfires, and damage resulting from these fires is associated with habitat development.

Landscape-level

At the landscape-level, as well as creating large ecological reserves, off-reserve conservation management is required with the key elements necessary for saproxylic beetle conservation being (modified from Lindenmayer *et al.* (2006)) protected areas within production forests; careful spatial and temporal arrangement of harvested stands; and appropriate fire management practices.

When designing the spatial and temporal arrangement of harvested stands within the wet forest to maintain diversity, a useful guide can result from combining the knowledge of the landscape created by natural disturbance with the habitat requirements and geographical distribution of saproxylic species. Wildfires create a mosaic of different sized areas of multi-aged and single aged dynamic stands, with

varying levels of fire-damage to both standing trees and woody debris. Forest landscape management (Lindenmayer *et al.* 2006) can try to replicate this as closely as possible, by varying the intensity of silvicultural practices in different areas and varying the size of harvested stands. Spatial and temporal continuity throughout the landscape can be better maintained by landscape planning such as positioning harvested areas with high intensity (such as CBS) next to areas harvested with a low intensity (such as partial harvesting) or reserved areas, both in terms of physical distance and time.

Ideally, the geographical range of species needs to be considered when designing reserves, so greater consideration can be given to species with a large proportion of their range within production forests. Currently the geographical range is known for only a few species, and this is likely to remain the case for the near future, advocating again the need for a precautionary approach to forest management. One approach may be to determine if there are any particular biodiversity hotspots of saproxylic beetles that can be protected.

Appropriate fire management across the landscape is a crucial feature of sustainably managed forest. One approach to maintain fire in the production forest would be to allow retained aggregates (if that silvicultural regime were adopted) to be burnt during the harvested coupe regenerative burn.

Salvage logging after wildfires has often been conducted to offset economic losses due to the burning of stands. Following salvage logging ecosystems are often worse affected than by either conventional logging or the initial disturbance with alterations occurring to stand structural complexity, ecosystem processes (hydrology, nutrient cycles, soil formation), and to the composition and abundance of species (Lindenmayer and Noss 2006; Lindenmayer and Ough 2006). Salvage logging removes potentially important structural elements and substrates such as fire-damaged trees (which often form hollow-bearing trees and may also be habitat for fire-adapted species (Chapter 7)), leaving a stand that is more akin to CBS disturbance than to wildfire disturbance. Thus, if salvage logging is implemented in production forests the same consideration should be given to the spatial and temporal arrangement as to forest harvested by CBS silviculture (as previously detailed).

8.5 RECOMMENDATIONS FOR RESERVE MANAGEMENT FOR SAPROXYLIC BEETLE CONSERVATION

This study highlights the importance of fire as an agent of hollow formation (Chapter 2, 6 and 7); and the association between some saproxylic beetles species and the specific habitats created by fire (Chapter 7). As discussed in detail in Chapter 7, CBS silviculture creates some habitats resembling wildfire (exposed burnt woody debris), but does not create others such as shaded burnt woody debris, fire-damaged and fire-killed standing trees. These elements are an important component of the landscape formed with a 'natural' wildfire disturbance regime, and any changes in their availability need to be considered.

Concerns due to changes in the occurrence, scale, frequency, intensity and overall impact of wildfires within the southern wet forests since European settlement and forest harvesting have been previously raised. Brown (1996) drew attention to the issue of fire management within the south-western Tasmanian world heritage area, where the simple model of 'benign neglect', and letting wildfires take there own course, would not be sufficient to ensure the survival of some fire-sensitive species (such as the endemic Huon pine (*Lagarostrobos franklinii*) and King Billy pine (*Athrotaxis selaginoides*) (Brown 1988, 1996)); nor the survival of some fire-dependant species (such as the nationally endangered orange bellied parrot (Brown and Wilson 1984) in the altered ecosystem.

Changes in the dynamics of fire throughout the landscape may alter the availability of hollow-bearing trees. Fire damage can aid the creation of hollows within a tree; however it can also reduce the number of hollow-bearing trees by causing the death and collapse of hollow-bearing or potentially hollow-bearing trees (Adkins 2006). One approach to maintain both hollow-bearing trees and fire-damaged substrate (which some saproxylic beetle species may depend on- Chapter 7) is to employ a flexible management system, where designated reserved areas and production forest areas can be altered depending on the regions of forest that have been burnt in a wildfire.

8.6 Summary

On the basis of the findings from this thesis, management recommendations are made that, if implemented, would demonstrate a more pre-emptive approach to saproxylic biodiversity conservation in production forests. In general, efforts should be made to ensure that long-term structural complexity is enhanced beyond levels which will eventuate under the current silvicultural practices. This could be achieved by introducing variability in harvesting intensity and mature tree retention levels, in rotation length and in coupe size. At the landscape level, management planning should consider maintaining sufficient spatial connectivity and temporal continuity of a range of tree age-classes to ensure the maintenance of the dependent fauna. Appropriate fire-disturbance management needs to be considered in relation to the role of fire as a habitat creator and destroyer.

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