

BROWN ROT IN INNER HEARTWOOD: WHY LARGE LOGS SUPPORT CHARACTERISTIC SAPROXYLIC BEETLE ASSEMBLAGES OF CONSERVATION CONCERN

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Abstract—It is not clear why large diameter logs generally host saproxylic beetle assemblages that are different from those of small diameter logs. In a study in Tasmanian wet eucalypt forest, two size-classes of *Eucalyptus obliqua* logs (>100cm and 30-60cm diameter) were destructively sampled to assess their beetle fauna and the associations of this fauna with decomposing wood. Ninety species were collected as adults from 42 logs; at least 19 species were also collected as larvae. The two log size-classes differed in beetle assemblage composition. These differences could be explained by the observation that certain beetle species were associated with specific successional phases of decomposing wood (rotten wood types). Those that were preferentially found in brown rotted heartwood, which was common in large logs, were rare or absent in small logs. This rotten wood type seems to be a relatively stable microhabitat and accordingly, the four most strongly associated species (in the genera *Cossonus*, *Dryophthorus*, *Prostomis* and *Pycnomerus*) seem likely to have low dispersal ability. Although relatively common in this habitat, each belongs to a genus whose European counterparts have undergone drastic range reductions. Our research highlights the importance of a level of landscape planning in Tasmanian forestry, which would maintain sufficient large diameter logs in the landscape over the long term.

INTRODUCTION

Saproxylic beetle assemblages have been studied in many forest ecosystems, including the boreal forests of Scandinavia (reviewed in Siitonen 2001) and Canada (Hammond and others 2004), the temperate forests of Germany (Kleinvoß and others 1996), the Douglas Fir forests of Northwest U.S. (Edmonds and Marra 1999, Maser and Trappe 1984), and the wet eucalypt forests of Tasmania (Yee 2005). These studies demonstrate that large diameter logs host specific saproxylic beetle assemblages that are not found in smaller sized logs. The ecological processes that shape these assemblages and create the differences between large and small diameter logs are not well understood. Differences in the decomposition pathways in large and small logs, resulting in differences in rotten wood types that potentially represent different microhabitats, may influence the saproxylic beetles assemblages within those logs.

Rotten wood is defined here as wood that has undergone some degree of decomposition. Decomposition results from either one or a combination of biotic and abiotic agents (Harmon and others 1986). These include mechanical, physical-chemical processes, and the physical and metabolic actions of various organisms (Kaarik 1974, Kirk and Cowling 1984, Swift 1977). They include bacteria (Clausen 1996), xylophagous arthropods (Carpenter and others 1988, Edmonds and Eglitis 1989), basidiomycete and ascomycete fungi, and micro-arthropods (Ausmus 1977, Seastedt 1984, Sollins and others 1987, Swift 1977). Depending on the types of processes and organisms, the physical, chemical and biological wood properties change in a specific way (Rayner and Boddy 1988). This gives rise to a specific rotten wood type that can

be described by its wood microstructure and chemistry, relative density, moisture content and nutrient levels (Ausmus 1977, Christensen 1984, Harmon and others 1986, Swift and Boddy 1984). To illustrate, brown rotted wood arises when 'brown-rot' fungi selectively remove cellulose and hemicellulose from the wood, leaving a residue of slightly modified lignin. By contrast, 'white-rot' fungi utilise all components of the wood cells, removing lignin, cellulose and hemicellulose and leaving the wood bleached, with a spongy, stringy or laminated structure (Kaarik 1974).

Current studies have clearly established that for the hardwood species *Eucalyptus obliqua* in Tasmanian wet eucalypt forests, large (>100 cm diameter) and small (30-60 cm diameter) logs at an intermediate decomposition stage differ in both type and spatial arrangement of rotten wood (Yee 2005). Eleven distinct rotten wood types have been classified within these logs. Although little is known of the actual decomposition processes or of the organisms involved, each type may result from a specific decomposition pathway and potentially provides a unique microhabitat for saproxylic beetles. Large diameter logs have a higher frequency of brown rotted heartwood occurring within the log centre. In small diameter logs a white rotten wood commonly occurs in the outer regions of the log. The presence of the different types of rotten wood demonstrates differing decay processes occurring in each size class of log. In large diameter logs internal decay probably established when the tree was alive, as heartrot is frequent in large old trees. Younger (smaller diameter) trees are less likely to give rise to logs with pre-existing heart rot, but such logs were more frequently rotted in their outer regions.

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Many saproxylic beetles are specially adapted to and intimately associated with the microhabitats and microclimates that occur in rotten wood (Dajoz 2000, Gilbertson 1984, Haack and Slansky 1987, Lawrence 1989, Speight 1989). For instance, in Japan the lucanids *Ceruchus lignarius* and *Aesalus asiaticus* occur more frequently in wood decomposed by brown rot fungi, whilst *Platycerus acuticollis* prefers wood decomposed by soft rot fungi (Araya 1993). Some beetle species rely on the actions of certain wood decay fungi to process and precondition the wood. Fungi can provide metabolic water and vitamins necessary for insect development, and they can produce enzymes for cellulose digestion that can be ingested by insects living within the wood. Fungi can detoxify wood that contains toxic or repellent allelochemicals, or decompose the wood to a softer and more chewable resource that can be more readily assimilated (Hanula 1996—see references within, Swift and Boddy 1984).

Saproxylic beetles may also be indirectly associated with one or more rot types through their dependence on organisms that are more intimately associated with a specific type of rot (Dajoz 2000, Speight 1989). For example, some elaterid beetles specifically prey on tipulid flies that only live in the moist wood invaded by white rot fungi (Dajoz 2000). The European *Elater ferrugineus* (Elateridae) is a predator of scarab beetles that occur in the red rotted wood of old trees (Svensson and others 2004).

In this study we investigated the saproxylic beetle assemblages found in large and small diameter logs in the wet eucalypt forest of Tasmania. Our aim was to determine whether the differences observed in the beetle assemblages between log size classes could be explained by associations between beetles and rotten wood types specific to a log size class.

METHODS

Study Location and Experimental Design

The study was conducted in wet eucalypt forest (Ashton 1982), at three localities in Tasmania's Southern Forests (fig. 1). These were in the Huon Valley, at the Warra Long Term Ecological Research (LTER) site (43°04'S, 146°41'E); in the Picton Valley, 10 km south of Warra; and in the Arve Valley, 10 km east of Warra. There were seven study sites among the three localities: four sites in single aged native forest that had regenerated from 'clearfell, burn and sow' silviculture (Hickey and others 2001) during the 1960s, and three sites in multi-aged unlogged forest that had regenerated following wildfires in the early 1900s. Within each site, three pairs of large and small *Eucalyptus obliqua* logs were sampled, and these were at an intermediate decomposition stage. In the logging regenerated forests, the studied logs were from felled trees left after the harvest. In the mature-unlogged forests, it was not possible to determine the date of tree fall but logs for the trial were selected so as to be of the same decomposition stage as those selected in the logging regenerated forests. The effect of forest type was not analysed in this study, but will be reported elsewhere (Yee 2005). Large logs were defined as those greater than 100 cm in diameter, derived from an 'old growth' tree; and small logs were 30-60 cm, derived from a 'regrowth' tree.

Sampling Method

Two 1 m sections were sampled from each log, with one to two hours being spent sampling each log section. Sections were taken along the base and middle positions of the fallen tree trunk, and were at least 4 metres apart (figs. 2A and 2B). The surface of each section was examined and then the section was removed from the log using a chainsaw. The removed section was then cut into three parts to allow ease of handling. Each part was then further cut up using an axe and hammer. Because of the gross differences in volume between the log size classes, for large diameter logs only one eighth of each 1-m long section was sampled (fig. 2B). Reducing the sampled volume ensured a more comparable sampling effort between log sizes and made sampling large logs logistically feasible.

The rot types present within each section were categorised according to 11 previously characterised Rotten Wood (RW) types (see table 1). The classification system for RW types of *Eucalyptus obliqua* logs had been developed alongside this study (Yee 2005), on the basis of colour, texture, hardness and 'RW region'. RW region to some extent indicates where decomposition may have started, for example, within the log or on the log surface. This was based on the consistent spatial association of a rot type with one of five areas within the log cross-section, and the direction from which the decomposition appeared to be spreading. The five areas specified were surface (sapwood), outer heartwood, inner heartwood, localised pockets from which the decay did not appear to spread, and throughout the heartwood (fig. 3). Colour was taken as indicative of the predominant type of fungal decay in process at the time of sampling: a 'white' or a 'brown' rot.

Beetle collection was conducted with the aid of a head torch and forceps to search within the log section as it was broken up. Collected adult and larval beetles were immediately preserved in 80 percent ethanol. To minimise impacts on saproxylic beetle populations, only subsets of specimens were taken when multiple individuals of the same species were found. Additional samples of larvae with host wood were taken to the laboratory for rearing, to allow identification and to observe life history. Beetles were sorted and identified to known species using various taxonomic keys, consulting with taxonomic experts, and comparing voucher specimens with material in the Australian National Insect Collection (ANIC: CSIRO Entomology, Canberra) and Tasmanian Forest Insect Collection (TFIC: Forestry Tasmania, Hobart). Specimens have been lodged at both, but with the primary set of vouchers lodged at the TFIC.

Statistical Analyses

Data and general statistical techniques—Presence-absence data were used instead of abundance because it was considered more relevant for determining a species' association with RW type. Using such an approach also reduced the influence of factors relating to the breeding strategy and the aggregative behaviour of individual species and the confounding effects of variable sampling efforts among the different RW types. Many larvae could not be identified even to family level, were seldom encountered, and may be the larval stage of some adult beetles. Therefore, species occurring only as larvae were documented separately and excluded from statistical analyses. Larval Elateridae and Scirtidae were the

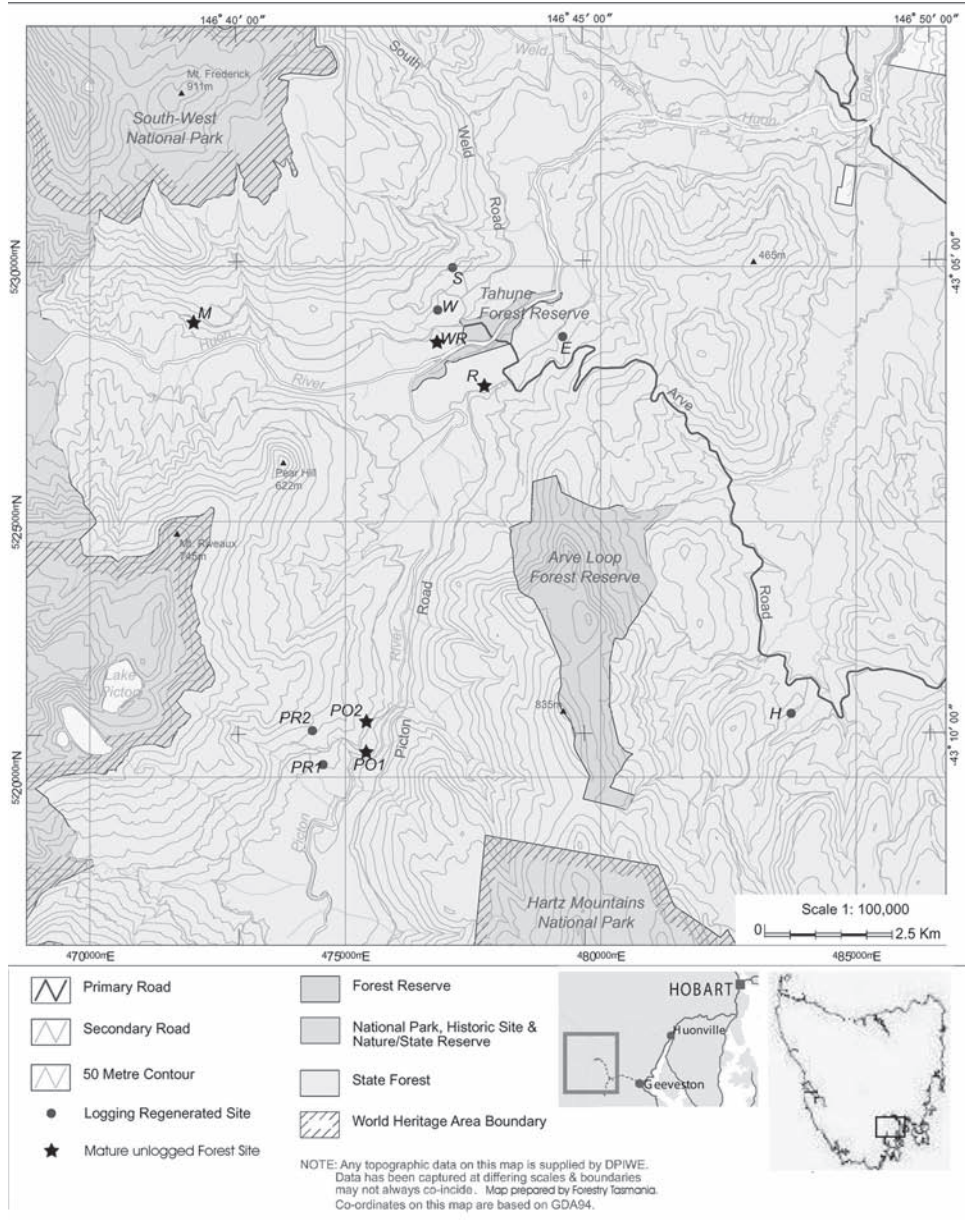


Figure 1—Location of the three study areas and seven sites in southern Tasmania, showing the State forest and forest reserve boundaries.

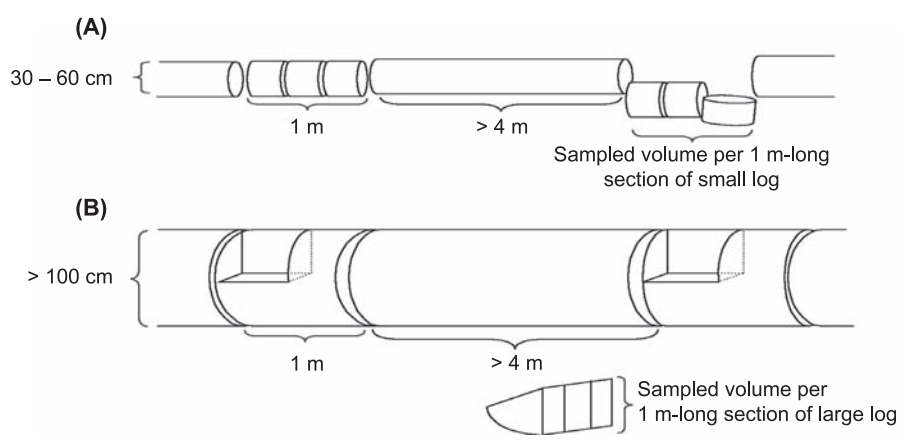


Figure 2—Schematic diagram of the destructive sampling method used for (A) small and (B) large diameter logs in wet eucalypt forests in southern Tasmania.

Table 1—Classification of 11 rotten wood types, listed in order by rotten wood origin, from *Eucalyptus obliqua* logs in wet eucalypt forests in southern Tasmania.

| Rotten wood type | Rotten wood origin | Suspected main decomposition process | Apparent decay type |
|--------------------------------|--------------------|--------------------------------------|---------------------|
| Fibrous surface rot | Surface (sapwood) | Fungal decay | Unknown |
| White jelly surface rot | Surface (sapwood) | Fungal decay | Unknown |
| Yellow dry slatey rot | Outer heartwood | Fungal decay | Unknown |
| White pocket rot | Outer heartwood | Fungal decay | White |
| White stringy rot ^a | Outer heartwood | Fungal decay | White |
| Brown spongy cubic rot | Outer heartwood | Fungal decay | Brown |
| Discolored wood | Heartwood | Unknown | NA |
| Wet cracks | Localised | Mechanical and other | NA |
| Brown blocky crumbly rot | Inner heartwood | Fungal decay | Brown |
| Red brown blocky fibrous rot | Inner heartwood | Fungal decay | Brown |
| Brown mudgut rot | Inner heartwood | Insects, fungal and other | Brown |

NA = not applicable.

^a During incipient stages of decomposition, this rotten wood type appears as dark crimson discoloured wood.

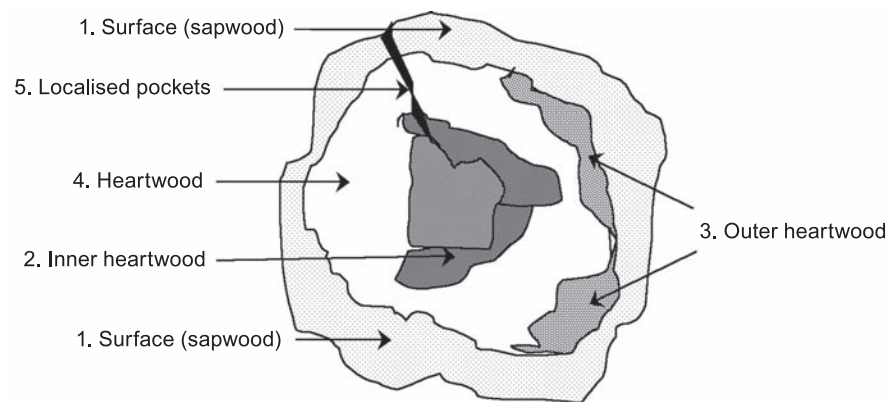


Figure 3—Stylised *Eucalyptus obliqua* log cross section showing the five main areas where rotten wood occurred, referred to as "RW region" in this paper.

exception. They were included because for these families, only larvae inhabit the log so there was no risk of double-counting. Furthermore, elaterids and scirtids are a common and important component of the saproxylic community, and are relatively easy to identify to family and morphospecies.

Two multivariate statistical methods were used, Non-metric Multidimensional Scaling (NMS) and Multi-Response Permutation Procedures (MRPP). NMS is a non-parametric ordination technique that relates the similarity of entities (e.g., logs or rotten wood samples), based on ranked distances, in multidimensional space (McCune and Grace 2002). NMS was performed using a Sorensen (Bray-Curtis) distance measure, in *PC-ORD* (McCune and Mefford 1999), choosing the 'slow and thorough autopilot' mode. MRPP in *PC-ORD* is a non-parametric method that uses permutation procedures for testing the hypothesis of no difference between two or more *a priori* groups based on multi-species data. This method provides a test statistic, T, which describes the separation between groups: the more negative the T, the stronger the separation. It also provides a p-value, which evaluates whether the observed difference is greater than expected by

chance. As recommended in the program, the method was run on an Euclidean distance measure and used the natural group weighting of $n/\text{sum}(n)$.

Comparison of beetles between log size classes—The frequency of occurrence of individual beetle species was compared between large and small logs, using Chi-square analyses. Data comprised the presence-absence of a species within a log pooled from all RW types from both log sections. Only common species (occurring in more than 25 percent of logs) were analysed. Beetle assemblages in large and small logs were graphically compared using NMS. Beetle species occurrences and RW type vectors were overlaid onto the ordination as a joint plot. RW type data comprised the presence-absence of RW types within a log, pooled from the two 1 m-long sections. MRPP were used to test for differences in beetle assemblage composition between log size-classes.

Beetle associations with RW types/regions—Individual beetle species and assemblages were investigated for their association with RW types. Data comprised the presence-absence of species within a RW type, pooled from both log

sections. Since many species were absent from over 20 percent of RW types per log, many standard statistical analyses, such as Chi-square analysis, would not have been reliable. Therefore interpretation of this aspect is limited to a discussion of observed trends on larval feeding and on species associations with rotten wood. NMS was used to determine whether RW types were characterised by similar beetle assemblages. MRPP were used to test whether the assemblages within rotten wood differed significantly among RW types. As RW region was found to be an important difference between large and small logs, species associations with RW region were also examined by overlaying RW region onto the ordination plot instead of RW type, and by testing group differences using MRPP. Beetle species vectors were also overlaid on the ordination plot as a joint plot.

RESULTS

In total, 90 species of adult beetles from 23 families were collected (appendix A). The most species-rich families were Staphylinidae (16 species), Curculionidae (12 species) and Carabidae (12 species). At least 19 of these species were also collected as larvae (appendix A), their identities being confirmed following successful larval rearing. Only 14 species occurred in over 25 percent of logs, and all of these were collected in both life stages, except *Aleocharinae* TFIC sp 34 (Staphylinidae) and *Exeiratus* TFIC sp 01 (Curculionidae), which were only collected as adults.

In total, 27 morphospecies were collected as larvae only (appendix B). Some of these may have represented the larval stages of species also collected as adults. Those larvae identified as species in the families Lycidae, Cantharidae, Cleridae and Melandryidae were not represented in the collection as adults. However, many of these larvae were only represented as singletons.

Comparison of Beetles between Log Size Classes

Sixty-three species of adult beetles were collected from large logs and 65 from small logs, with 38 species common to both. Of the 14 species that occurred in over 25 percent of logs, *Cossonus simsoni* (Curculionidae) occurred only in large logs, and *Pycnomerus* TFIC sp 02 (Zopheridae) and *Coripera deplanata* (Tenebrionidae) were significantly more frequent in large logs than in small ones ($p = 0.013$ and 0.0278 respectively) (fig. 4). Meanwhile, *Enneaphyllus aeneipennis* (Cerambycidae) only occurred in small logs.

Results from the NMS (figs. 5A and 5B) and MRPP showed that large and small logs differed significantly in their beetle assemblages (fig. 5B, separation along Axis 3; $p = 0.001$, $T = -4.5$). Ten small logs were clearly different from the cluster of large logs. Overlaying the beetle species onto the ordination plot revealed that *Enneaphyllus aeneipennis* had a strong influence on this pattern, correlating with Axis 3 ($r^2 = 0.65$). Several species correlated in the opposite direction: *Prostomis atkinsoni* (Prostomidae) ($r^2 = 0.31$), Elateridae TFIC sp 21 (Elateridae) ($r^2 = 0.24$), *Dryophthorus* TFIC sp 01 (Curculionidae) ($r^2 = 0.25$), *Pycnomerus* TFIC sp 02 (Zopheridae) ($r^2 = 0.20$) and Scirtidae YEE sp 04 (Scirtidae) ($r^2 = 0.23$). Two RW types, 'brown mudgut rot' and 'wet cracks', which are both wet RW types, also correlated with this axis ($r^2 = 0.24$ and 0.20 respectively).

Beetle Associations with RW Types and Origins

The relative frequencies of individual species differed among RW types. No species was restricted to a single RW type but some showed preferences for either a RW region or for an amalgamation of RW types into decay type (white or brown) (table 2). For example, the xylophagous species *Dohrnia simplex* (Oedemeridae), *Dryophthorus* TFIC sp 01, *Prostomis atkinsoni*, *Cossonus simsoni* and *Pycnomerus* TFIC sp 02 preferred the brown rotten heartwood (inner) types, whilst

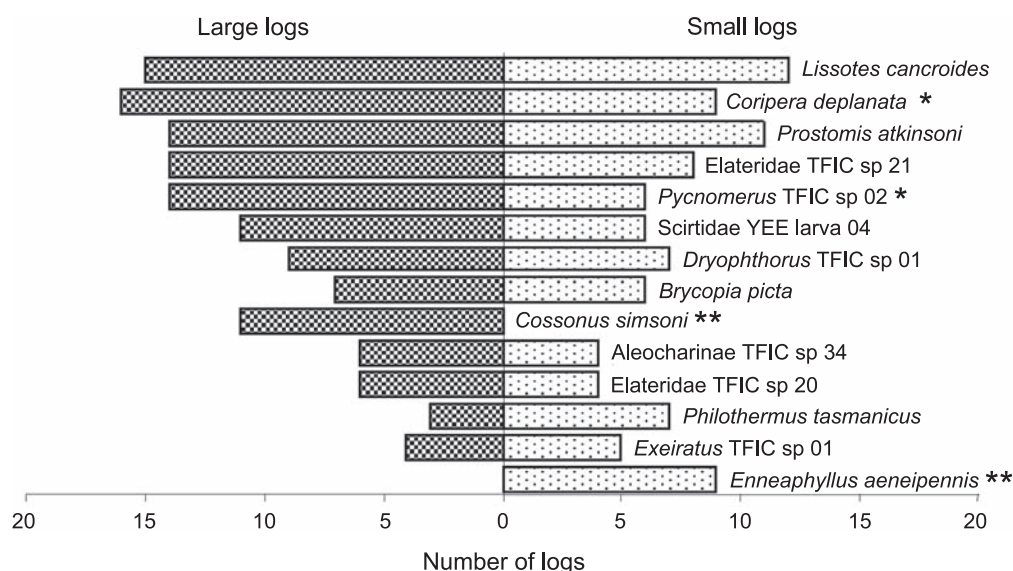


Figure 4—The frequency of common (> 25 percent of logs) saproxylic beetle species found in 21 large (left) and 21 small (right) *Eucalyptus obliqua* logs from wet eucalypt forests in southern Tasmania. Species whose occurrences differed significantly ($p < 0.05$) between the two log size classes are denoted by *, while those exclusive to a particular log size class are denoted by **.

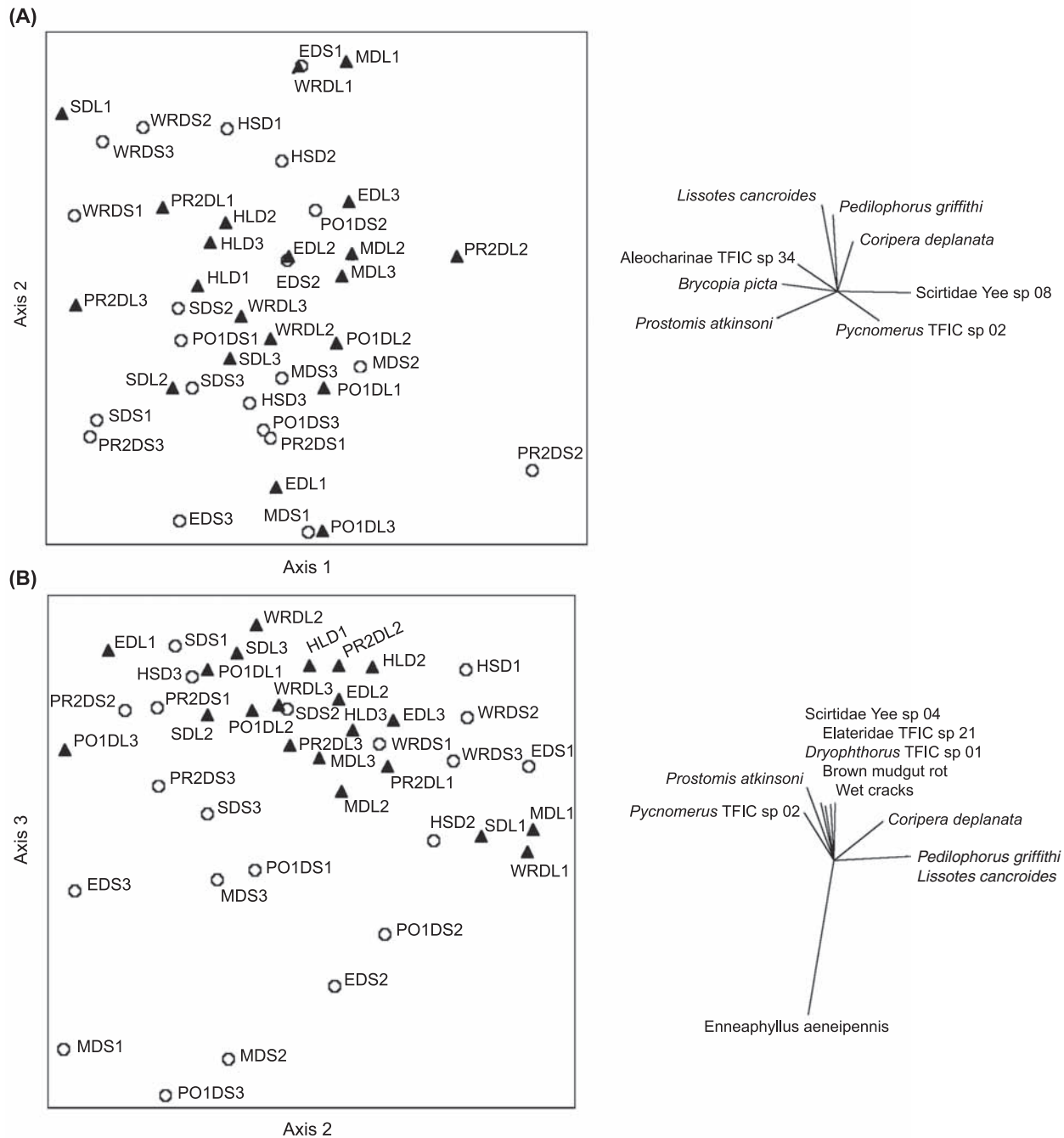


Figure 5—NMS ordination showing saproxylic beetle assemblages from 21 large (▲) and 21 small (○) *Eucalyptus obliqua* logs from wet eucalypt forests in southern Tasmania. (A) axes 1 and 2; (B) axes 2 and 3. Based on presence-absence data for saproxylic beetle species pooled from two 1-m long sections per log (single occurrences were excluded). Alphanumeric codes are log identification tags. Vectors based on beetle species occurrence and rotten wood type (refer to table 2) are overlaid as a joint plot; for greater clarity, these are displayed adjacent to the ordination. Stress = 0.18, $p = 0.0196$. Vector scaling 100 percent. Only vectors with $r^2 > 0.2$ are shown.

Enneaphyllus aeneipennis preferred the white rotten heartwood types. Two further xylophagous species *Coripera deplanata* and *Lissotes cancroides* (Lucanidae) were more closely associated with surface (sapwood) rotten wood than with other log areas, but their occurrence also extended into the brown rotten heartwood (inner). The saprophagous species *Scirtidae YEE sp 04* (Scirtidae) was more frequent in the very wet RW types ('wet cracks' and 'brown mudgut rot'). The

xylophagous *Syndesus cornutus* (Lucanidae) was restricted to brown rot, where many larvae were found feeding within brown rotted wood that was either cubic or crumbly, and occurring in either inner or outer heartwood.

Except for the distinct patterns evident for two single RW types ('brown mudgut rot' and 'fibrous surface rot'), there were no discrete clusters of the same RW type evident in ordination

Table 2—Species associated with rotten wood type, grouped by rotten wood origin and apparent decay type

| RW origin ^a | SF (SP) | | OH | | | | H | IH | | | L | Total |
|---------------------------------------|---------|-----|-----|-----|-----|-----|----|-----|-----|-----|----|-------|
| | WJR | FSR | YDR | WPR | WSR | BSR | DW | RBR | BBR | BMR | WC | |
| RW type ^b | WJR | FSR | YDR | WPR | WSR | BSR | DW | RBR | BBR | BMR | WC | Total |
| Apparent decay type ^c | – | – | – | Wh | Wh | Br | – | Br | Br | Br | – | Total |
| <i>Lissotes cancroides</i> | 8 | 14 | 2 | 1 | 2 | 1 | 6 | | | 3 | | 37 |
| <i>Prostomis atkinsoni</i> | 1 | 2 | | | 2 | 2 | 5 | 6 | 5 | 11 | 2 | 36 |
| <i>Coripera deplanata</i> | 7 | 16 | | 1 | | 1 | 3 | 1 | | 4 | | 33 |
| Elateridae TFIC sp 21 | 5 | 9 | | | | 2 | 4 | 3 | 2 | 4 | | 29 |
| <i>Dryophthorus</i> TFIC sp 01 | 2 | 5 | | | 1 | | 1 | 8 | 1 | 7 | | 25 |
| <i>Pycnomerus</i> TFIC sp 02 | | 2 | | | | 1 | 6 | 6 | 2 | 7 | | 24 |
| <i>Cossonus simsoni</i> | 1 | 4 | | 1 | | 1 | 4 | 7 | | 4 | | 22 |
| Scirtidae YEE sp 04 | | 1 | | | 1 | | 2 | 1 | 2 | 7 | 9 | 22 |
| <i>Diemenoma</i> TFIC sp 01 | | 3 | | | 1 | 1 | 3 | 4 | 3 | 2 | | 17 |
| Aleocharinae TFIC sp 34aA | 3 | 4 | | | | 1 | 2 | | 1 | 1 | | 12 |
| <i>Enneaphyllus aeneipennis</i> | | 2 | | 2 | 5 | | 2 | | | 1 | | 12 |
| <i>Dorhnia simplex</i> | 1 | | | | | | 1 | 4 | 2 | 3 | | 11 |
| <i>Exeiratus</i> TFIC sp 01 | | 2 | | 1 | 2 | | | 3 | | 3 | | 11 |
| Aleocharinae TFIC sp 13 | 1 | 2 | | | | | 2 | 1 | 1 | 3 | | 10 |
| Elateridae TFIC sp 20 | 2 | 7 | | | | | | | | 1 | | 10 |
| <i>Philothermus tasmanicus</i> | 1 | 1 | | | 1 | | 2 | | | 3 | 2 | 10 |
| <i>Syndesus cornutus</i> | 1 | | | | | 3 | 1 | 3 | | 1 | | 9 |
| <i>Pedilophorus griffithi</i> | | 7 | | | | | | | | 1 | | 8 |
| <i>Promecoderus tasmanicus</i> | 1 | 6 | | | | | 1 | | | | | 8 |
| <i>Trechimorphus diemenensis</i> | | 1 | | | | 1 | 2 | 2 | | 2 | | 8 |
| <i>Adelium abbreviatum</i> | 2 | 4 | | | | | 1 | | | | | 7 |
| <i>Stichonotus leai</i> | 2 | 4 | | | 1 | | | | | | | 7 |
| Denticollinae TFIC sp 01 | 1 | | | | | | | 1 | | 3 | 1 | 6 |
| Elateridae TFIC sp 23 | 2 | 1 | | | | | 2 | 1 | | | | 6 |
| <i>Dryocora cephalotes</i> | | | | | | | 1 | 1 | 1 | 2 | | 5 |
| Elateridae TFIC sp 19 | | | | | | | 1 | 2 | | 2 | | 5 |
| <i>Lissotes subcaeruleus</i> | 2 | | | | | | 1 | | | 2 | | 5 |
| <i>Macroplectus</i> CHANDLER 'Type 1' | | 1 | | | | | 1 | | 1 | 1 | 1 | 5 |
| Scirtidae YEE sp 02 | | | | | | | | | | 4 | 1 | 5 |
| Scirtidae YEE sp 08 | | | | | | | 1 | | | 2 | 2 | 5 |
| <i>Scopodes intermedius</i> | 1 | 3 | | | | | 1 | | | | | 5 |
| <i>Sloaneana tasmaniae</i> | 1 | 2 | | | | | 1 | 1 | | | | 5 |
| Staphylinidae ANIC 88-0088 | 1 | 2 | | | | | 1 | 1 | | | | 5 |
| <i>Toxeutes arcuatus</i> | | | | | | 1 | 1 | 1 | | 2 | | 5 |
| Curculionidae YEE sp 49 | | | | | | | 3 | | | 1 | | 4 |
| <i>Dinichus terreus</i> | | 3 | | 1 | | | | | | | | 4 |
| Staphylininae TFIC sp 03 | 1 | 1 | | | | | 2 | | | | | 4 |

RW = rotten wood.

^a SF (SP) = surface (sapwood); OH = outer heartwood; IH = inner heartwood; H = heartwood; L = localised.

^b WJR = white jelly surface rot; FSR = fibrous surface rot; YDR = yellow dry slaty rot; WPR = white pocket rot;

WSR = white stringy rot; BSR = brown spongy cubic rot; DW = discoloured wood; RBR = red brown soft blocky fibrous rot; BBR = brown blocky crumbly rot; BMR = brown mudgut rot; WC = wet cracks.

^c Wh = white rot; Br = brown rot.

Number within a cell represents the number of logs in which a species occurred. Grey cells highlight more than two occurrences. Species are listed in decreasing order of most to least frequency. Species with fewer than four occurrences were excluded.

plots based on beetle assemblages (figs. 6A and 6B). That is, no single RW type had a distinct beetle assemblage. Despite this apparent lack of difference among single RW types, MRPP suggested that there were highly significant differences ($p < 0.000001$, $T = -11.4$). The ordination was re-examined by overlaying the RW region on the ordination instead of RW type, and this showed that some RW regions formed discrete clusters (figs. 7A and 7B), and this difference among RW regions was significant ($p < 0.000001$, $T = -17.6$). Species that correlated with the ordination included those that showed an association when examining individual species (table 2): *Prostomis atkinsoni* and *Pycnomerus* TFIC sp 02 were associated with the brown rotten heartwood (inner) types, *Lissotes cancroides* and *Coripera deplanata* with the surface (sapwood) RW types, and *Enneaphyllus aeneipennis* with the white rotten heartwood types.

DISCUSSION

Our results support the hypothesis that the differences in saproxylic beetle assemblages between large and small logs can be explained by the discrete decompositional processes undergone in logs of the two size classes, as reflected in the region or type of rotten wood. For example, we have shown in a concurrent study that types of brown rotten heartwood occur more frequently in large logs (Yee 2005). This study has described the clear association of two beetle species (*Cossonus simsoni* and *Pycnomerus* TFIC sp 02) with brown rotten heartwood. It is therefore reasonable to assume that one explanation for their specificity to large logs (in this study) is due to the presence of these RW types not commonly found in small logs. This argument is also supported by other related observations. Members of the family Scirtidae apparently prefer large logs (this study, Yee 2005; Grove and Bashford 2003). These beetles appear to be associated with the ‘wet’ RW types, such as ‘wet cracks’ and ‘brown mudgut rot’, which were more frequent in large logs (Yee 2005). Their association can be explained by their requirement for wet habitats, as larval scirtids have retained an ancestral respiratory system adapted for living in saturated environments and mouthparts designed for filtering wet detritus (Lawrence and Britton 1994). Meanwhile, the white rotten heartwood types are more frequent in small logs than in large logs (Yee 2005). In this study, one beetle species (*Enneaphyllus aeneipennis*) was restricted to this particular white rot type, and was only detected in small logs.

These log size preferences and rotten wood type associations could only be demonstrated for common species, as these occurred in sufficient numbers for statistical analysis. In theory, rarity can be positively related to habitat specificity (Rabinowitz 1981), so it seems likely that many of the less common species in this study will also have a preference for log size and/or rotten wood type preference. However, additional sampling would be needed to gain an adequate understanding of the habitat preferences of naturally rare species.

There may have been factors other than the types of rotten wood to which species may be responding. For example, the xylophagous *Coripera deplanata* was more frequent in large logs, yet showed an association for the surface (sapwood) rotten wood that is common to both log sizes. It may have preferred large logs because the sapwood layer is thicker on

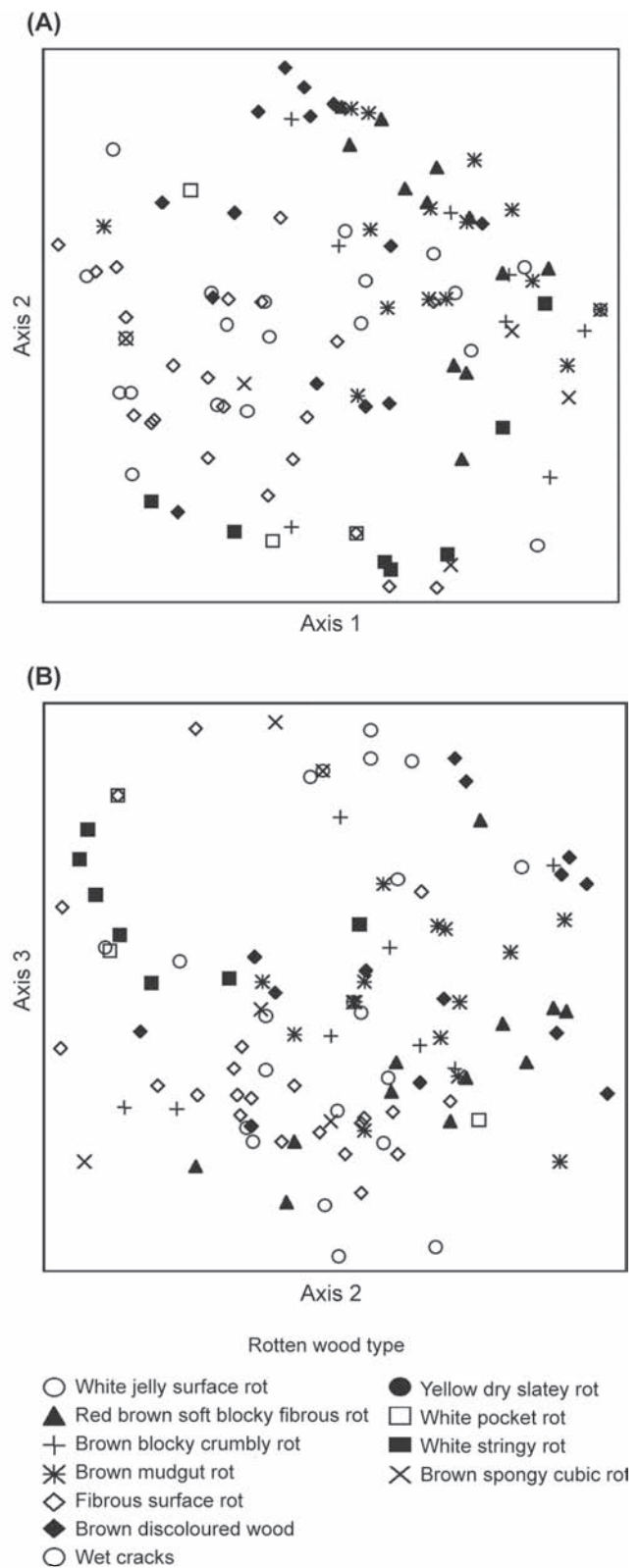


Figure 6—NMS ordination of saproxylic beetle assemblages from 119 samples of rotten wood from 42 *Eucalyptus obliqua* logs, from wet eucalypt forests in southern Tasmania, with rotten wood type (symbols) overlaid. (A) axes 1 and 2; (B) axes 2 and 3. Based on presence-absence data of 42 beetle species within a rotten wood type pooled from two 1-m long sections per log (doubletons excluded). Stress = 0.23, $p = 0.0196$. Samples of rotten wood with no beetles were omitted.

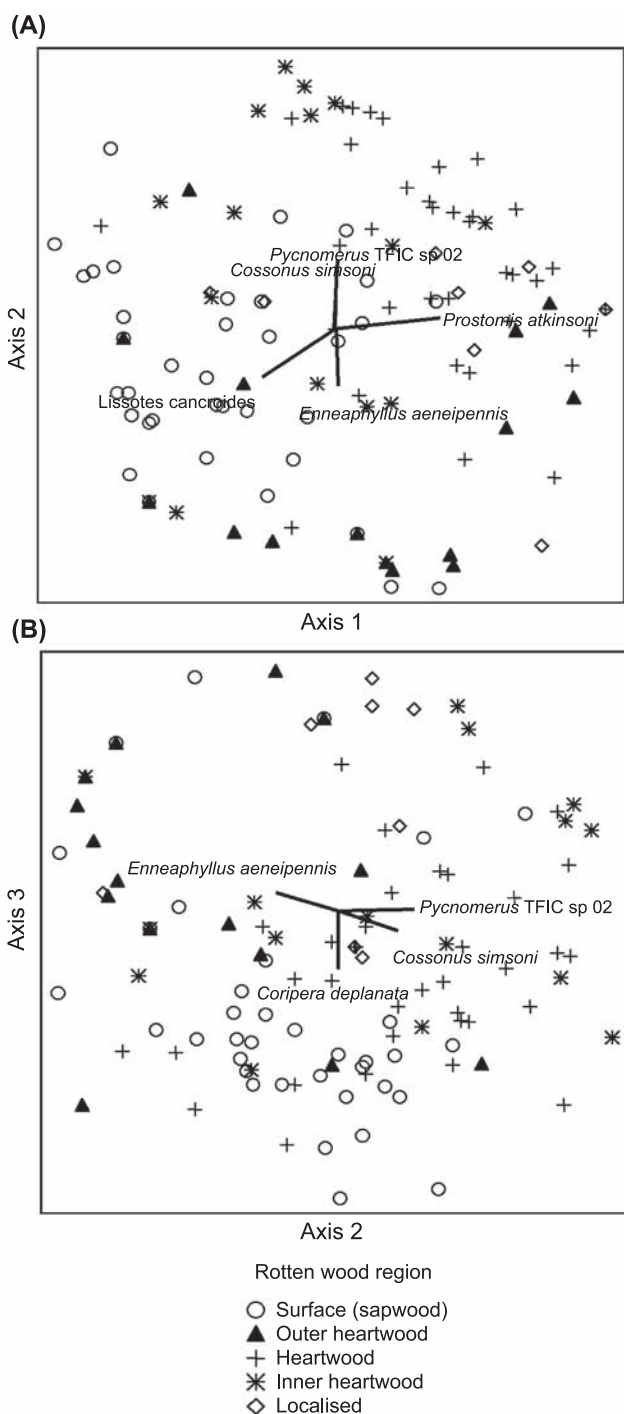


Figure 7—Same ordination as in figure 6, but with rotten wood region (symbols) overlaid. (A) axes 1 and 2; (B) axes 2 and 3. Vectors are defined by beetle species occurrence data. Vector scaling 100 percent. Only vectors with $r^2 > 0.2$ are shown.

large logs than small logs (Brack and others 1985). This is the case for the northern European sapwood feeding *Pytho kolwensis* (Pythidae) which, in a Finnish study, preferred large spruce logs over small logs for this reason (Siitonen and Saaristo 2000). Another interpretation is that *Coripera deplanata* seems to have relatively broad larval habitat associations, also occurring in the brown rotted heartwood (inner

common in large logs (Unpublished data. Dr. Simon Grove, Conservation Biologist, Forestry Tasmania, 79 Melville Street, Hobart, Tasmania, Australia). Additional sampling might reveal a better understanding of the mechanisms underlying its apparent preference for large logs.

Whatever the limitations of our study, the findings suggest that the brown rotted heartwood is an important habitat feature of large *Eucalyptus obliqua* logs. Its value may lie in its relative stability as a habitat. Habitat stability is defined as how favourable it remains for a population over a continuous period of time (Southwood 1977). In general, large logs of the size-dimensions studied here are considered to offer more stable habitats for saproxylic beetles than do smaller sized logs (Grove and Meggs 2003). This is because they tend to take longer to decompose, partly because of lower decay rates (Harmon and others 1986, Mackensen and others 2003, Stone and others 1998), and so persist longer in the landscape; they maintain more optimal moisture levels (Amaranthus and others 1989) that allow buffering against the effects of desiccation and temperature extremes; and they provide potential refuges during disturbance events, such as wildfire (Meggs and Taylor 1999, Michaels and Bornemissza 1999). In the present study, it is suspected that the brown rotted heartwood had probably originated in the living tree, entering through infection courts such as those caused by fire damage or the breakage of large branches (Greaves and others 1965, Tamblin 1937, Wardlaw 2002). Therefore as a habitat, it might begin to sustain an assemblage of beetles from the time of tree-fall or even beforehand, thus allowing more time to sustain assemblages of species dependent on this habitat. The rotten wood in small logs, on the other hand, almost certainly owed its origin to fungal and microbial colonisation since the tree-fall event.

The apparently poor dispersal potential of species associated with the brown rotted heartwood also supports the notion that this is a relatively stable habitat for saproxylic beetles. Theoretically, species dependent on stable habitats should require lower dispersal abilities, while those in less predictable habitats would require higher ones (Southwood 1977). Species that were clearly associated with the brown rotted heartwood (*Cossonus simsoni*, *Prostomis atkinsoni*, *Dryophthorus* TFIC sp 01 and *Pycnomerus* TFIC sp 02) have characteristics that appear to fit this pattern. They are all small xylophagous species, often found living in aggregates, appeared to have sedentary behaviour and were either flightless, relatively long living or a combination of these. All except *Prostomis atkinsoni* are flightless, and flightlessness is one outcome of habitat stability (Lattin and Moldenke 1990, Stevens 1997). *Prostomis atkinsoni*, *Dryophthorus* TFIC sp 01 and *Pycnomerus* TFIC sp 02 seem capable of undergoing successive generations within the same log without emerging, and this interpretation is supported for *Prostomis atkinsoni* by a recent study that found genetically similar individuals at very fine spatial scales (Watson 2003). Adults and larvae of *Prostomis atkinsoni*, *Dryophthorus* TFIC sp 01 and *Pycnomerus* TFIC sp 02 subsisted in the original host wood material for over 25 months in the laboratory, with both adult and larval stages still alive. Furthermore, these three species were collected from partially decomposed to well-rotted inner heartwood, thus showing their capacity to feed on a broad range of decomposed wood stages; and in the laboratory

they seemed to re-ingest previously consumed wood. The specificity of several of these beetle species for habitat types more common in large logs, coupled with their apparent low powers of dispersal, suggests that these species are likely to be susceptible to reductions in large logs, and the subsequent fragmentation effects that can result from intensive forestry (Nilsson and Baranowski 1997, Ranius and Nilsson 1997).

In Northern Europe, the declines in saproxylic beetles that have resulted from centuries of timber harvesting and recent intensive forest management (Grove 2002) provide examples of what may occur in Australian production forests if similar management trajectories were followed. Remarkably, each of the four species specific to the brown rotted heartwood (*Dryophthorus* TFIC sp 01, *Prostomis atkinsoni*, *Cossonus simsoni*, and *Pycnomerus* TFIC sp 02) belongs to a genus whose European representatives have already experienced drastic declines, with some regional extinctions. And yet, in this Australian (Tasmanian) study, they were among the most common species collected. Moreover, some of the European species appear to have similar rotten wood type preferences to those in this study. For example, *Dryophthorus corticalis*, which lives in the red heartwood rot of old standing and fallen oak (*Quercus* sp) trees, is threatened in Great Britain (Hyman 1992), Germany (Bense 2002), and the Czech Republic (Strejcek 1996). *Prostomis mandibularis*, which occurs in the red-brown muddy rot of decomposing oak logs (personal observation), is extinct in the UK (Boswijk and Whitehouse 2002) and threatened with extinction in parts of Germany (Bense 2002). A number of species from the genus *Cossonus* are threatened in several European countries: *Cossonus linearis* in central Europe (Harde 1984) and the Czech Republic (Strejcek 1996); *C. cylindricus* in Finland (Martikainen 2001); and *C. parallelepipedus* in the Czech Republic (Strejcek 1996) and Germany (Bense 2002). *Pycnomerus terebrans*, which occurs in the red rotten wood of old hardwood trees, has also become extinct in Britain (Buckland and Dinnin 1993), and is close to extinction in parts of Germany (Wenzel 2002). Considering the similarities found in this study with those of Northern European examples, it seems likely that developing an understanding of the dispersal ecology of these species will provide valuable information as to how to manage large logs over appropriate spatial and temporal scales, to ensure that such major declines and extinctions can be avoided in Tasmania and elsewhere.

In conclusion, large *Eucalyptus obliqua* logs in Tasmanian wet eucalypt forests were found to host an assemblage of beetle species that was rarely encountered in small logs, and this could be explained by the more general presence of brown rotten heartwood (inner) types within large logs. This rotten wood type had probably originated in the standing tree; however the specific decomposer organisms or processes involved in its development are unknown. Current research projects are attempting to address this issue (Harrison and others 2003a, Hopkins and others 2003) (Unpublished data. Dr. ZiQing Yuan, Plant Pathologist, Department of Primary Industries, Water and Environment, Newtown Laboratories, 13 St Johns Avenue, Newtown, Tasmania, Australia 7008). It seems that this rotten wood type is a relatively stable microhabitat, and species associated with it appear to have low dispersal potential. Considering that these species belong to genera whose European representatives have undergone

serious declines, it seems they may also be susceptible to the long-term effects of intensive forest management and fragmentation. Determining how far these species disperse, whether they colonise the living tree, or at which stage they colonise the fallen log, and for how long they remain within the log, will provide valuable information as to how to manage for large logs over appropriate spatial and temporal scales. Current research projects are seeking to answer some of these questions (Harrison and others 2003b, Watson 2003). A caveat to this study is that the conclusions have mostly been drawn from the commonly collected species, and so conservation issues relating to naturally rare species still need to be addressed.

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APPENDIX A

Taxonomic list of adult saproxylic beetles hand collected from 42 *Eucalyptus obliqua* logs in wet eucalypt forests in southern Tasmania.

| Family and subfamily | Species |
|-----------------------------|--|
| Carabidae-Migadopinae | <i>Stichonotus leai</i> (Sloane 1910) |
| Carabidae-Trechinae | <i>Sloaneana tasmaniae</i> (Sloane 1915) |
| Carabidae-Trechinae | <i>Trechimorphus diemenensis</i> (Bates 1878) |
| Carabidae-Broschinae | ^a <i>Promecoderus tasmanicus</i> (Castelnau 1867) |
| Carabidae-Callistinae | <i>Lestignathus sp nr foveatus</i> (Sloane 1920) |
| Carabidae-Lebiinae | <i>Agonocheila curtula</i> (Erichson 1842) |
| Carabidae-Pentagonicinae | <i>Scopodes intermedius</i> (Blackburn 1894)? |
| Carabidae-Psydrinae | <i>Amblytelus</i> TFIC sp 01 |
| Carabidae-Psydrinae | <i>Theprisa convexa</i> (Sloane 1920) |
| Carabidae-Pterostichinae | <i>Notonomus politulus</i> (Chaudoir 1865) |
| Carabidae-Pterostichinae | <i>Rhabdotus reflexus</i> (Chaudoir 1865) |
| Carabidae-Zolinae | <i>Pterocyrtus tasmanicus</i> (Castelnau 1867) |
| Ptiliidae | Ptiliidae TFIC sp 04 |
| Leiodidae-Cholevinae | <i>Nargomorphus jeanneli</i> (Szymczakowski 1963) |
| Leiodidae-Cholevinae | <i>Nargomorphus</i> TFIC sp 02 |
| Scydmaenidae | Scydmaenidae TFIC sp 04 |
| Scydmaenidae | Scydmaenidae TFIC sp 08 |
| Scydmaenidae | Scydmaenidae TFIC sp 10 |
| Staphylinidae | Staphylinidae ANIC 88-0088 |
| Staphylinidae-Pselaphinae | <i>Macroplectus</i> CHANDLER 'Type 1' |
| Staphylinidae-Pselaphinae | <i>Macroplectus tasmaniae</i> Raffray |
| Staphylinidae-Pselaphinae | <i>Startes</i> CHANDLER 'Tasmania 1' |
| Staphylinidae-Pselaphinae | <i>Tasmanityrus newtoni</i> (Chandler 1987) |
| Staphylinidae-Tachyporinae | <i>Sepedophilus</i> TFIC sp 01 |
| Staphylinidae-Aleocharinae | Aleocharinae TFIC sp 13 |
| Staphylinidae-Aleocharinae | Aleocharinae TFIC sp 25 |
| Staphylinidae-Aleocharinae | Aleocharinae TFIC sp 27 |
| Staphylinidae-Aleocharinae | Aleocharinae TFIC sp 28 |
| Staphylinidae-Aleocharinae | Aleocharinae TFIC sp 34 |
| Staphylinidae-Scaphidiinae | <i>Scaphidium</i> YEE sp 01 |
| Staphylinidae-Paederinae | <i>Hyperomma bryophilum</i> (Lea 1923) |
| Staphylinidae-Paederinae | Paederinae TFIC sp 03 |
| Staphylinidae-Staphylininae | <i>Quedius</i> TFIC sp 04 |
| Staphylinidae-Staphylininae | Staphylininae TFIC sp 03 |
| Lucanidae-Syndesinae | ^a <i>Syndesus cornutus</i> (Fabricius 1801) |
| Lucanidae-Lucaninae | ^a <i>Lissotes cancroides</i> (Fabricius 1787) |
| Lucanidae-Lucaninae | ^a <i>Lissotes curvicornis</i> (Boisduval 1835) |
| Lucanidae-Lucaninae | <i>Lissotes subcaeruleus</i> (Bomans 1986) |
| Scarabaeidae-Melolonthinae | <i>Heteronyx pilosellus</i> (Blanchard 1850) |
| Scarabaeidae-Melolonthinae | ^a <i>Phyllochlaenia</i> TFIC sp 01 |
| Scarabaeidae-Melolonthinae | <i>Phyllochlaenia villosus</i> (Le Guillou 1844) |
| Scarabaeidae-Melolonthinae | <i>Telura vitticollis</i> (Erichson 1842) |
| Scirtidae | <i>Prionocyphon?</i> TFIC sp 01 |
| Scirtidae | <i>Pseudomicrocara atkinsoni</i> (Waterhouse 1877)? |
| Byrrhidae-Byrrhinae | <i>Pedilophorus griffithi</i> (Lea 1907) |
| Byrrhidae-Byrrhinae | <i>Pedilophorus</i> nr ANIC sp 88-0313 |
| Eucnemidae | <i>Neocharis tasmanicus</i> (Muona 1987) |
| Elateridae-Pityobiinae | <i>Tasmanelater pelionensis</i> (Calder 1996) |
| Elateridae-Agrypninae | <i>Agrypnus</i> TFIC sp 01 |
| Elateridae-Denticollinae | Denticollinae TFIC sp 01 |

(continued)

APPENDIX A

Taxonomic list of adult saproxylic beetles hand collected from 42 *Eucalyptus obliqua* logs in wet eucalypt forests in southern Tasmania—continued

| Family and subfamily | Species |
|--------------------------------|--|
| Elateridae-Denticollinae | Denticollinae TFIC sp 16 |
| Elateridae-Denticollinae | <i>Elatichrosis exarata</i> (Candeze 1863) |
| Elateridae-Denticollinae | <i>Enischnelater</i> TFIC sp 01 |
| Elateridae-Elaterinae | <i>Augenotus quadriguttatus</i> (Erichson 1842) |
| Cleridae-Phyllobaeninae | <i>Lemidia</i> YEE sp 02 |
| Nitidulidae-Cryptarchinae | <i>Cryptarcha laevigata</i> |
| Silvanidae-Brontinae | <i>Cryptamorpha</i> TFIC sp 01 |
| Silvanidae-Brontinae | <i>Cryptamorpha victoriae</i> (Blackburn)? |
| Cryptophagidae-Cryptophaginae | <i>Cryptophagus tasmanicus</i> (Blackburn 1907) |
| Cryptophagidae-Cryptophaginae | <i>Cryptophagus</i> sp nr <i>gibbipennis</i> (Blackburn 1892) |
| Cerylonidae-Ceryloninae | ^a <i>Philothermus tasmanicus</i> (Slipinski 1988) |
| Corylophidae-Corylophinae | ^a <i>Holopsis</i> TFIC sp 01 |
| Corylophidae-Sericoderinae | <i>Sericoderus</i> TFIC sp 05 |
| Zopheridae-Zopherinae | <i>Docalis funerosus</i> (Hope 1845) |
| Zopheridae-Pycnomerinae | <i>Penthelispa fuliginosa</i> (Erichson 1842) |
| Zopheridae-Pycnomerinae | ^a <i>Pycnomerus</i> TFIC sp 02 |
| Zopheridae-Colydiinae | <i>Enhypon tuberculatus</i> |
| Tenebrionidae-Lagriinae | ^a <i>Adelium abbreviatum</i> (Boisduval 1835) |
| Tenebrionidae-Lagriinae | <i>Brycopia coelioides</i> (Pascoe 1870) |
| Tenebrionidae-Lagriinae | <i>Brycopia hexagona</i> (Carter 1920) |
| Tenebrionidae-Lagriinae | ^a <i>Brycopia picta</i> (Pascoe 1869) |
| Tenebrionidae-Lagriinae | ^a <i>Coripera deplanata</i> (Boisduval 1835) |
| Tenebrionidae-Zolodininae | ^a <i>Tanylypa morio</i> (Pascoe 1869) |
| Prostomidae | ^a <i>Dryocora cephalotes</i> (Waterhouse) |
| Prostomidae | ^a <i>Prostomis atkinsoni</i> (Waterhouse 1877) |
| Oedemeridae | ^a <i>Dohrnia simplex</i> Champion |
| Cerambycidae-Prioninae | ^a <i>Enneaphyllus aeneipennis</i> (Waterhouse 1877) |
| Cerambycidae-Prioninae | ^a <i>Toxentes arcuatus</i> (Fabricius 1787) |
| Curculionidae | <i>Curculionidae</i> YEE sp 49 |
| Curculionidae-Cryptorhynchinae | <i>Decilaus lateralis</i> (Lea 1913) |
| Curculionidae-Cryptorhynchinae | <i>Decilaus</i> nr <i>striatus/subfasciatus</i> |
| Curculionidae-Cryptorhynchinae | <i>Poropterus antiquus</i> Boheman |
| Curculionidae-Cryptorhynchinae | <i>Tyrtaeosus ustulatus</i> Pascoe |
| Curculionidae-Dryophthorinae | <i>Dryophthorus</i> ECZ sp 02 |
| Curculionidae-Dryophthorinae | ^a <i>Dryophthorus</i> TFIC sp 01 |
| Curculionidae-Molytinae | ^a <i>Dinichus terreus</i> (Pascoe 1887) |
| Curculionidae-Molytinae | <i>Exeiratus</i> TFIC sp 01 |
| Curculionidae-Cossoninae | Cossoninae TFIC sp 06 |
| Curculionidae-Cossoninae | ^a <i>Cossonus simsoni</i> (Lea 1910) |
| Curculionidae-Cossoninae | <i>Pentarthrum</i> TFIC sp 01 |

^aRefers to species that were also collected in their larval form.

APPENDIX B

Taxonomic list of larval saproxylic beetles hand collected from 42 *Eucalyptus obliqua* logs in wet eucalypt forests in southern Tasmania.

| Family | Larval morphospecies code: <i>Genus</i> |
|---------------|---|
| Carabidae | CARLAR15 |
| Carabidae | CARLAR8 |
| Staphylinidae | LAR5: <i>Scaphidium</i> sp |
| Scirtidae | Scirtidae YEE sp 04 |
| Scirtidae | Scirtidae YEE sp 08 |
| Byrrhidae | LAR29 |
| Eucnemidae | EUCNEM2 |
| Elateridae | Elateridae TFIC sp 23 |
| Elateridae | Elateridae TFIC sp 19 |
| Elateridae | Elateridae TFIC sp 20 |
| Elateridae | Elateridae TFIC sp 21 |
| Elateridae | Elateridae YEE sp 06 |
| Elateridae | LAR33 |
| Elateridae | ELAT1 |
| Lycidae | LYCIDLAR1 |
| Cantharidae | LAR11 |
| Cantharidae | LAR3 |
| Cleridae | CLER2: <i>Lemidia</i> sp |
| Melandryidae | LYMEX1: <i>Mystes</i> sp |
| Tenebrionidae | LAR10 |
| Tenebrionidae | LAR16 |
| Tenebrionidae | TENLAR1 |
| Indet | LAR30 |
| Indet | CURLAR2 |
| Indet. | CARLAR9 |
| Indet. | STAPHLAR1 |
| Indet. | STAPHLAR7 |
