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# Biology and conservation ecology of selected saproxylic beetle species in Tasmania's southern forests



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A research thesis submitted in fulfilment of the requirements  
for the degree of Doctor of Philosophy  
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Chapter 4 is presented as a manuscript and was submitted for publication to *Biodiversity and Conservation* on the 30th of September 2013. The three authors and their subsequent contribution to the manuscript (shown as a percentage) are as follows:

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I dedicate this thesis in loving memory of my grandfather James W. G. Yaxley.

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## ABSTRACT

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Many saproxylic beetle species (those associated with dead wood) are considered to be threatened by intensive forest management, yet few have been subjected to autecological studies that might help in their conservation. For this thesis, two lines of research were followed to investigate the autecology of six species thought to be vulnerable to intensive forestry. The study was carried out in the wet-eucalypt production forests of southern Tasmania.

The first line of research explored methodologies that could be used to help understand life-history and feeding traits of log-dwelling beetles, in order that the resultant autecological information might be used as input into models of species persistence. Study 1a investigated the sexual development and life-history strategies of two sympatric species of stag-beetle, *Lissotes menalcas* and *L. cancroides*; and study 1b used molecular approaches to explore the feeding relationship of a mycophagous saproxylic beetle *Prostomis atkinsoni* and its putative food source, 'gingerbread rot'. Both studies in this line of research provided useful methodological insights. Additionally, the findings from study 1a suggest that coexistence of *L. menalcas* and *L. cancroides* may be enabled by their differing patterns of sexual development across seasons; while the findings of study 1b were equivocal, in that numerous fungal species were detected in the gut-contents of adult and larval *P. atkinsoni* but few were found in both; furthermore, there was little overlap in the mycota of beetles' guts and gingerbread rot. Unexpectedly, some species of basidiomycete known to be wood-rotters were found in the guts but not in the gingerbread rot itself.

The second line of research comprised predictive modelling approaches at the level of (a) microhabitat (coarse woody debris) and (b) site and landscape, both aimed at identifying the habitat requirements of all six species and exploring the possibility of making reasonable predictions about the species' occurrence at each of these spatial scales. In study 2a, models performed well in relating the probability of occurrence of each of the six beetle species to the presence or absence of particular suites of rotten-wood types. The addition of site-scale variables did not greatly enhance the models' abilities to predict occurrence of the six species of beetles, but at this level, forest stand structure and age of

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regeneration generally contributed the most explanatory power. In study 2b, geology, aspect, and time since last fire were good predictors of beetle occurrence across the study-area, although predictive ability may have been inflated by overfitting and autocorrelation. Overall, the models indicate that in unharvested forest these beetles tend to preferentially occur (within their chosen rotten-wood types) in multi-aged stands with a mature eucalypt element, while their continued occurrence in forest regenerating following clearfelling may be explained by their occupation of ‘legacy’ coarse woody debris derived from the previous unharvested stand.

The findings from both lines of research provide clear pathways for future exploration and modelling of species persistence in production-forest landscapes, and could help guide management practices accordingly, particularly in relation to the required spatial and temporal arrangement of mature forest.

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## CHAPTER 1 GENERAL INTRODUCTION

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Dead wood is recognised as an important component of forest ecosystems, providing habitat that supports a diverse and specialised invertebrate community. Research into dead wood and its management originated in Europe where there exists an extensive literature on the ecology of dead wood in forest ecosystems. In Tasmania, however, our understanding of the dynamics and management of dead-wood resources is still in its infancy. Even though the forests of Europe and southern Australia differ in numerous ways, the European perspective on dead wood and its importance in forest ecosystems can provide a base of knowledge from which to formulate general hypotheses regarding the role and dynamics of dead wood in Tasmania. It is considered important to appraise Europe's current knowledge of dead-wood dynamics and management in boreal coniferous forest from Scandinavia and temperate deciduous forests further south in Europe, and to compare these findings with our understanding of the ecology of Tasmania's wet-eucalypt forests.

Saproxylic beetles are useful indicator species to gauge how well dead wood is managed, particularly in areas of intensive forest management (Speight 1989; Siitonen 2001). These beetles spend all or a part of their life cycle inside dead wood, a habitat which provides for them, protection, a food source and a potential nursery for their young. Saproxylic beetles are important ecosystem engineers, improving the health of forest ecosystems by breaking down dead wood and putting nutrients back into the soil. Hence, it is imperative that we understand the environmental and management factors that influence the survival and long-term persistence of this group of species in forest ecosystems. As noted above, research on the ecology and conservation of saproxylic beetles originates largely from European forest ecosystems, while knowledge of the ecology of saproxylic beetles in Tasmania's forests is severely lacking. The overall aim of this thesis is to augment our knowledge of the ecology, conservation, and response to forest management practices of saproxylic beetles in Tasmania's wet-eucalypt forests. As an initial step towards this aim, this chapter reviews the state of knowledge of the role and dynamics of saproxylic beetles in European forest ecosystems. Some North American examples are given because this region has also contributed to our understanding of saproxylic beetles.

### **1.1.1 What is dead wood?**

The creation of dead wood begins at an early stage in a tree's life. In fact, only the outer parts of the tree trunk are alive, supplying nutrients to other cells for growth. The internal duramen or heartwood, meanwhile, is comprised of dead woody cells that provide structure and support. Hence, a greater proportion of the tree's organic matter is derived from dead woody cells than from those of living cells (Cavalli and Mason 2003). The continuous production of dead woody tissue means that over a long period of time, a tree can amass large amounts of dead wood. As the dead wood decays these 'older' trees will lose their structure and stability, making them susceptible to uprooting or to losing branches. The dead wood that exists on the forest floor is comprised not only of dead trees and lost limbs but also of dead wood that is created by natural disturbances, such as disease, fire, wind or storms (Parks 1999; Mountford 2002), or by anthropogenic disturbances, such as timber harvesting (Harmon 2001; Grove and Meggs 2003). Trees or branches that have fallen as a consequence of either natural or man-made impacts may initially, if young, reveal little evidence of internal decay. However, once a branch or tree has been torn from its live source, it is then (in the more traditional sense) considered to be dead wood and will carry on decaying. Hence, in this study, to distinguish between the non-living parts of a living tree and 'dead wood', dead wood is defined as any piece of wood that is detached from the living tree.

For the purposes of research and forest inventories, dead wood is normally categorised according to its diameter (Waddell 2002; Woldendorp *et al.* 2002): fine woody debris (FWD) measures less than 10 cm in diameter, while coarse woody debris (CWD) measures more than 10 cm in diameter (Kruys and Jonsson 1999; Woldendorp *et al.* 2002; Rainus *et al.* 2003). Both FWD and CWD include dead wood that is formed by broken or uprooted dead trees, fallen trunks and decaying old hollow trees (Cavalli and Mason 2003).

### **1.1.2 Why is dead wood so important?**

#### **1.1.2.1 Dead wood as a carbon store**

Dead wood represents at least decades, and often centuries, of carbon fixation, such that slowly growing and decaying trees can sequester carbon for tens to thousands of years (e.g. Scotts Pine: Dudley and Vallauri 1996). For example, a

Russian study examining dead-wood dynamics in a series of permanent and temporary forest plots at different successional stages and different disturbance regimes, reported that the average residence time of carbon was 22-30 years (Krankina and Harmon 1995). Stored carbon was also quantified in Tasmanian forests by Moroni *et al.* (2011) who found that the mass of carbon in standing trees on 1.5 M ha of Tasmanian State forest was 163 Tg (teragram) C, with 139 Tg C derived from eucalypt forest.

As dead wood acts as both a source and a store of carbon, it is an important component of the forest carbon cycle, and an important pool when accounting for carbon stocks and fluxes in forest ecosystems (Woldendorp *et al.* 2002). However, of all the major forest carbon pools (overstorey and understorey trees, other vegetation, litter and soil) it is the least studied (Dudley and Vallauri 1996). Nevertheless, under the requirements of the 1992 Kyoto Protocol demanding countries to undertake national carbon inventories, studies into this crucial component of the carbon cycle are increasing (Dudley and Vallauri 1996; Woldendorp *et al.* 2002).

#### **1.1.2.2 Dead wood as a slow-release fertiliser**

Dead wood is comprised of organic matter that represents a long period of nutrient uptake by the live tree. Although nutrient stocks of sodium, phosphorus, nitrogen, calcium and magnesium in dead wood are relatively small (Wilcke 2005), as the dead wood decomposes, it slowly releases these nutrients back into the soil (McFee and Stone 1966; Edmond and Eglitis 1989). The speed at which the nutrients are put back into the soil depends on the rate of decomposition; warm, wet climates speed up decomposition rates of dead wood, while the opposite is true for cold, dry climates (Lambert *et al.* 1980; Harmon *et al.* 1986; Stockland 2001). Many organisms contribute to the decomposition process, principally fungi (Rayner and Boddy 1988) and bacteria (Clausen 1996), while invertebrates, such as saproxylic beetles, act as mediators of this process (Grove and Meggs 2003). For example, *Toxotes arcuatus*, a tenebrionid saproxylic beetle, has been described as an ecosystem engineer facilitating the breakdown of wood and the release of nutrients, and plays a vital role in wood decomposition and nutrient recycling (Wardlaw *et al.* 2009).

### 1.1.2.3 Dead wood as habitat for wildlife

Dead wood is regarded as having high species richness and the most biodiverse habitat in a healthy forest (Dudley and Vallauri 1996) because the degenerative processes that take place in dead wood provide a variety of microhabitats in which a varied and specialised fauna and flora can live (Elton 1966; Jonsson *et al.* 2005). Representatives of saproxylic species exist in almost every terrestrial insect order (Gunning 2000; Grove 2002b; Grove and Meggs 2003), with the largest proportion constituting members of the Coleoptera. An example of high species richness in saproxylic beetles is in old-growth forest in La Massane, France, where 37% of beetles sampled were associated with dead wood (Trave 2003), while in Finland, Martikainen *et al.* (2000) reported that 42% of 553 beetles species sampled in old spruce forest were saproxylic.

The hollows of dead or dying trees as well as logs on the forest floor provide important habitat for amphibians, reptiles, birds and mammals (Smith and Lindenmayer 1988; Bull 2002; Koch *et al.* 2009). Thomas (1979) surveyed the forests of the Blue Mountains of Oregon and Washington and identified 179 vertebrate species that use dead wood, representing 57% of the vertebrate species breeding there. Although vertebrates are not necessarily saproxylic obligates they use dead wood because it can provide them with shelter and food. In Tasmania, the little pygmy possum (*Cercartetus nanus*) shelters in downed dead wood while in torpor over the colder months (Duncan and Taylor 2001), as does the black bear (*Ursus americanus*) in North America (Bull 2002). Birds (particularly owls and woodpeckers) and also bats use dead wood for shelter, preferring standing dead trees (Bull and Holthausen 1993; Cavalli and Mason 2003), while amphibians and reptiles shelter in dead wood because of the high moisture-content and protection it provides (Bull 2002; Patrick *et al.* 2006). In addition, many species of birds and mammals feed on other organisms that inhabit dead wood. The foraging value of dead wood peaks during the mid to late stages of decay when the logs are softer and easier to break apart (Bull 2002). For instance, in the Pacific Northwest USA, the pileated woodpecker (*Dryocopus pileatus*) forages on decaying Douglas fir (*Pseudotsuga menziesii*), while red-back voles (*Myodes* spp.) forage extensively on fungi associated with dead wood in the later stages of decay (Ure and Maser 1982). In Australia, little is known about the extent to which vertebrates forage in dead wood, though black cockatoos are

commonly observed to excavate beetle larvae from dead standing timber. Signs of scratching and burrowing by vertebrates are evident on many logs in Australian forests, though assigning these signs to species is difficult.

Unsurprisingly, dead wood is host to many species of fungi that actively decompose wood. The decaying ability of wood-rotting fungi makes them an important part of the decomposition process, assisting in the return of nutrients into the soil and making the wood accessible to other species that would otherwise not be able to exploit the resource. In the Swiss Alps, a single hectare of spruce forest can support over 300 species of wood-rotting fungi (Dudley and Vallauri 1996). Moreover, the exposed fruiting bodies of many fungi are a food source for specialised feeders, such as flies and beetles (e.g. the European tenebrionid beetles, *Bolitiophagus reticulatus* and the IUCN red-listed *Oplocephala haemorrhoidalis*, live and feed on the polypore fungus, *Fomes fomentarius* (Sverdrup-Thygeson and Midtgaard 1998; Jonsson 2003; Jonsson *et al.* 2005).

Importantly, for some higher-plant species, dead wood is the main site for successful establishment of tree seedlings because it retains moisture and provides nutrients to the seedling (Harmon and Franklin 1989; Gray and Spies 1997; McKenny and Kirkpatrick 1999). A study conducted in the wet-eucalypt forests of southern Tasmania, showed that tree seedlings were more abundant on fallen logs than on the adjacent ground (McKenny and Kirkpatrick 1999). Dead wood also acts as a substrate for epixylic liverworts, mosses and lichens that attach themselves to the outer parts of dead wood, absorbing nutrients produced as the wood decays. A study of cryptogams on dead wood in the wet-eucalypt forests of Tasmania has shown that dead wood can support up to 165 epixylic bryophyte species (Turner 2003).

### **1.1.3 Different species of saproxylic beetles require different microhabitats in dead wood**

The physical attributes of dead wood influence the abundance and diversity of species that live inside it. Factors such as the tree species from which the log is derived, the log's diameter, its stage of decay, and degree of exposure can all alter the variety of microhabitats within the log environment and thus the range of species that will be found there. In addition, the tunnelling activity of beetles, and

amount and type of fungi mycelium in the wood also creates and alters the variety of microhabitats in dead wood.

Dead wood of different diameters support different suites of saproxylic species (Elton 1966; Kruys and Jonsson 1999; Siitonen and Saaristo 2000; Yee *et al.* 2001; Grove 2002a; Jonsson *et al.* 2005; Yee 2005). For example, the endangered beetle, *Pytho kolwensis*, inhabits logs of fallen spruce with a diameter greater than 20 cm (Siitonen and Saaristo 2000). The ecology of dead wood derived from trees with large diameters has received much attention from researchers because they decompose more slowly and can support larger numbers of individuals than smaller logs (Ober and Minogue 2010; Sweeney *et al.* 2010; Work and Hibbert 2010). Large-diameter logs exhibit greater internal to external ecological gradients and it is thought that this may be positively correlated with increased species richness because of the wider variety of specialised niches for saproxylic species to exploit (Yee 2005; Work and Hibbert 2010). In addition, the amount of solar radiation that dead wood receives may alter the species composition of a log by influencing the type and variety of microhabitats within it. For instance, some saproxylic beetles are shade-intolerant, preferring sun-exposed dead wood beneath open canopies (Peterken 1999; Jonsell *et al.* 2004; Lindhe *et al.* 2005).

Saproxylic invertebrates may also have a preference for dead wood that originates from particular tree species. A study on substrate requirements of saproxylic beetles in Sweden found that the number of species associated with different tree genera ranged from five to 202, with 174 species (32%) found associated with only one tree genus (Jonsell *et al.* 1998). In general, studies have found that beetle association with a tree host shows specificity at the level of genera and family (see Tavakilian *et al.* 1997 for an example in coleopterans).

Numerous studies have shown that saproxylic species are often dependent on wood at particular stages of decay (Grove and Meggs 2003; Janssen *et al.* 2011; Lassauce *et al.* 2012). Studies have also shown that saproxylic species often prefer particular types of rotten wood that exist within dead wood (Araya 1993; Stockland 2001; Yee 2005; Gilbertson 1984; Hopkins 2007). For example, in Tasmanian wet-eucalypt forests, rotten wood formed by brown-rot fungi have been shown to have specific saproxylic beetles associated with them (Yee *et al.* 2004, Chapter 5). To date, research on fungus-insect relationships has focused on

beetles that live inside the fruiting bodies attached to the outer parts of dead or decaying wood (Sverdrup-Thygeson and Midtgaard 1998; Jonsell and Norlander 2002), rather than the fungus-insect relationships that occur inside dead wood. Saproxylic species may not necessarily be associated with the fungi that create the rotten-wood type they inhabit. Rather, the existence of micro-organisms, such as bacteria, might determine the presence of a particular species, but very little is known about this subject.

The above examples highlight the specialised relationships that can exist between dead wood and saproxylic invertebrates. As different saproxylic species require different attributes from their dead-wood habitat there may be a need to manage species individually (Matern *et al.* 2007; Thomaes *et al.* 2008).

## ***1.2. European perspectives on the ecology and management of dead wood and the conservation of saproxylic species.***

### **1.2.1 Why is conservation and management of dead wood worthy of focussed study?**

#### **1.2.1.1 Current abundance of dead wood is no guarantee of future abundance**

Many European communities have been clearing and managing their forests for thousands of years. This has altered forests to a point where they no longer represent the ancient natural ones that once covered the greater part of Europe. Large-scale clearing of forest initially occurred for agricultural purposes, with many forests not cleared for agriculture later becoming managed timber forests (Warren and Key 1991; R  ther and Walentowski 2008; Williams 2008; Kaplan *et al.* 2009). The evolution of forest management regimes has had an enormous impact on the production and abundance of dead wood (Stokland and Larsson 2011).

The harvesting of timber over hundreds or, in some parts of Europe, thousands of years has resulted in forests that are much simpler in structure than their ancient counterparts and produce smaller amounts of dead wood (Mather 2001; Ritter 2011). Natural forests that are dynamic multi-aged, multi-structured ecosystems, affected by natural disturbances at appropriate intervals, with abundant, heterogeneous dead-wood resources (Elton 1966; Grove 2002b; Grove and Meggs



2003; Gibb *et al.* 2005) are now extremely rare, or even absent, in most western European countries. For example, extreme reductions in dead-wood volumes, of approximately 90–98%, have been reported in the production forests of Fennoscandia, over the past century (Sittonen 2001), while similar declines have been reported in many other European nations (e.g. as little as 0.6m<sup>3</sup>/ha of dead wood remains in the productive forests of Austria, (Dudley and Vallauri 1996)).

#### **1.2.1.2 Loss of dead wood means a decline in saproxylic species**

As a consequence of the loss of dead-wood resources from European forests much of Europe's saproxylic biodiversity is today threatened with extinction. For example, 39% (172 species) of Sweden's threatened beetle species require dead wood for their survival (Samuelsson *et al.* 1994), while hundreds of dead-wood-dependent species are listed as threatened within Fennoscandia and Britain (Berg *et al.* 1993; Warren and Key 1991; Komonen *et al.* 2008).

Of the entire dead-wood-dependent fauna, beetles are recognised as the group most vulnerable to the loss of dead wood. Strong evidence of this vulnerability is provided by Britain's sub-fossil record (e.g. peat deposits) that reveals that many saproxylic beetles became regionally extinct or underwent major declines following the historical deforestation of Western Europe (Warren and Key 1991; Whitehouse 2006). In 2010, the IUCN produced a comprehensive red-list identifying 436 threatened saproxylic beetles in Europe (Nieto and Alexandra 2010).

Saproxylic beetles exhibit unique life-history traits that appear to be a consequence of their specialisation in resource-poor dead wood habitat (i.e. low fecundity (small broods), long life spans, slow maturation rates, and often the loss of flight capabilities (e.g. *Lissotes* spp.). For example, the life cycles of the European saproxylic beetle, *Rosalia alpina* (Drag *et al.* 2011), and *Lucanus cervus* (Rink 2011) take at least three years to complete, while the endemic Tasmania lucanid, *Lissotes menalcas*, produces few eggs and is also thought to take a couple of years to complete its lifecycle (Karen Richards and Chris Spencer, unpublished data). Whilst there is very little published on life-history adaptations of saproxylic beetles, this slow life-history schedule is the likely result of the nutrient poor food source (decomposing wood) on which they survive. For instance, the quality of food resources for adults can greatly affect dispersal

potential, as seen in the beetle, *Osmoderma eremita* (Cetoniidae), whose body condition has a relationship with flight-related behaviour (Dubois *et al.* 2010). The scarcity of information regarding saproxylic beetle life cycles and their dietary needs makes it difficult to understand and predict how their populations will react to changing environmental factors. Nevertheless, a slow life-history schedule and poor dispersal abilities may also explain why saproxylic beetles appear so vulnerable to changes in the distribution and abundance of dead wood, as these traits increase the risk of extinction for small and isolated populations (Davies *et al.* 2008).

### 1.2.1.3 Changes in dead-wood management

Improvements in modern harvesting technologies and other forestry activities, coupled with an unprecedented demand for timber products, have resulted in the unsustainable exploitation of forest resources in recent times (foresters may argue that these ‘improvements’ allow them to better sustain wood supply, albeit not dead-wood habitat). These conditions have led to colossal losses of natural and semi-natural forests not only in Europe, but throughout the world. The remnant forest patches that survive harvesting become increasingly reduced, as do the dead-wood-dependent species that rely on their resources (Peterken 1999; Schiegg 2000; Kouki 2001; Rouvinen 2002). In the last decade, increased awareness of the importance of dead-wood habitat (Jonsson *et al.* 2006) in forest ecosystems, has driven research designed to aid the management of dead-wood habitat in landscapes degraded by timber harvesting and fragmented by agriculture (Grove 2002b; Davies *et al.* 2008). On-going negotiations between the timber industry, policy makers and biologists have resulted in management strategies designed to increase the volume of dead-wood habitat while maintaining an economically viable timber industry (Ranius *et al.* 2005; Jonsson *et al.* 2006). Such novel management practices are continually being refined as new research findings emerge (Hodge and Peterken 1998; Peterken 1999; Harmon 2001; Davies *et al.* 2008).

Although management practices vary among countries some general principles apply to all forest policies. The retention of old trees and dead wood on forest stands is a key principal of forest management for restoring dead wood (Dudley and Vallauri 1996; Butler *et al.* 1999; Cavalli and Mason 2003). Likewise,

retaining key habitats, such as corridors or clumps of remnant habitat between harvested stands, is also a widely applied management practice (including in Tasmanian forests: Taylor 1991; DFRD Technical Report 2009) that provides saproxylic species with the opportunity to disperse throughout the landscape (Schiegg 2000; Kouki 2001). The retention of habitat that includes old trees, middle-aged trees (to ensure continuity of dead wood) and fallen dead wood widely regarded as the best management practice to maintain the structural complexity of forest that is needed to ensure the continuity and spatial heterogeneity of dead-wood resources (Butler *et al.* 1999). An alternative strategy occasionally employed when it is difficult to retain dead wood habitat is to create it artificially. For example, in Norway and Sweden high cut stumps are left in logged areas or artificial snags are created (i.e. standing dead trees) leaving a proportion of some trunks standing after felling (Jonsell *et al.* 2004; Ranius *et al.* 2005; Gibb *et al.* 2006; Jonsson *et al.* 2006).

#### **1.2.1.4 Are current management recommendations for dead wood effective?**

Current prescriptions for managing dead wood (detailed above) are designed to provide and maintain dead-wood habitat in the short-term. However, there is little evidence to suggest that these management practices will conserve dead-wood habitat in the long-term (Davies *et al.* 2008). To ensure the continuous, long-term supply of dead wood, sufficient trees or patches of forest habitat must be retained both spatially throughout the landscape and temporally over long periods of time, so as to facilitate landscape-level habitat continuity (Grove 2002b). Unfortunately, current forest management recommendations ubiquitously focus on ‘site-based, small-scale studies, with short-term solutions’ (Davies *et al.* 2008). Although these studies monitor and describe changes in the saproxylic fauna in response to the application of management practices, they do so without long-term research to fill the gaps in our ecological knowledge, so they are only catering for the management of dead-wood habitat in the short-term.

Another issue in the effective management of dead-wood habitat are the costs involved in implementing management strategies, which can lead to conflict between those who wish to conserve this habitat and those who see wood solely as an important economic resource (Dangerfield *et al.* 2005; Ranius *et al.* 2005). Some methods are more cost-effective than others and offer a potential avenue for

comprise in such circumstances. For example, in central and northern Sweden (and elsewhere) it is inexpensive, and in fact, more economical to retain old dying trees than it is to harvest them (Ranius *et al.* 2005). On the other hand, the most effective strategy to improve dead-wood habitat (i.e. to prolong periods between harvesting by increasing rotation lengths; Ranius *et al.* 2005; Yee 2005), is one of the most expensive management options available. Ultimately, the choice of management techniques is determined by a combination of economic and environmental needs (Ranius *et al.* 2005). To date, however, there are few evidence-based conservation studies that demonstrate whether current management techniques for dead-wood habitat are effective and cost efficient in the long-term (Davies *et al.* 2008).

#### **1.2.1.5 Dead wood in Australia**

Little is known about the dynamics and attributes of dead-wood habitat in Australia. In particular, we still know very little about the extent of biodiversity that is supported by dead wood in Australian forest ecosystems. Europe and Australia share several saproxylic beetle genera, with some representatives of these genera that are listed as threatened or extinct in Europe being widespread in Australia (Yee *et al.* 2004). For example, *Prostomis atkinsoni* is common throughout Tasmania's southern wet-eucalypt forests, whereas its European counterpart, *Prostomis mandibularis*, is extremely rare throughout most of Europe, as a result of the reduction in dead wood through intensive forest management (Olsson and Lemdahl 2009). The taxonomic status of Australian saproxylic invertebrates is also very poorly defined with many species yet to be described (for example, there are currently two saproxylic species of *Dryophthorus* (Coleoptera: Curculionidae) in Tasmania awaiting taxonomic description) (Yee 2005). Hence, our understanding of the ecology of these species remains poor. Although experts believe that the proportion of Australia's saproxylic fauna threatened with extinction (under Commonwealth legislation) may be far less than that of Europe, it is nevertheless apparent that several Australian saproxylic species are in fact threatened by the loss of dead-wood habitat (Meggs and Taylor 1999, Meggs and Munks 2003). For example, Tasmanian beetles from the family Lucanidae (e.g. *Lissotes menalcas* and *L. latidens*) are suspected to be poor dispersers, with slow life-history schedules, and are thus, particularly sensitive to loss of dead-wood habitat (Meggs and Taylor

1999; Michaels and Bornemissza 1999; Meggs *et al.* 2003). More importantly, the European experience suggests that even common saproxylic species can readily become threatened (Warren and Key 1991). Evidence from the fossil record shows that many now-rare species were common several hundred years ago (Warren and Key 1991). The limited amount of research on dead-wood dynamics and habitat in Australia suggests that if we do not specifically address the management of this habitat, then we are likely to see the same scale of conservation problems as has occurred in Europe, with many species becoming threatened through loss of dead-wood habitat (Grove 2000; Grove 2002b). Therefore, many of the principles established overseas will mirror those needed here in Australia.

Several recent Australian studies on the dynamics and ecology of dead-wood habitat are beginning to rectify the knowledge deficit in this field (Koch *et al.* 2008; Wardlaw *et al.* 2009; Gates *et al.* 2010; Grove *et al.* 2011). Woldendorp *et al.* (2002) found that several forest types in Queensland, New South Wales and Tasmania contained greater amounts of dead wood than comparable European forests. Stamm (2006) developed models to explain the dynamics of coarse woody debris in Tasmanian forests to facilitate a better understanding of the ecology of dead wood habitat within tall lowland wet-eucalypt forests and found that decomposition may take longer than first thought. Grove *et al.* (2011) have further refined these models to examine logs of different diameters and their pathways of internal decomposition, concluding environmental factors such as exposure should be taken into account as well the physical characteristics of the log (e.g. log diameter). These studies provide the first attempts to predict the dynamics of dead wood resource in Australian forests; knowledge that is necessary to better manage the abundance and heterogeneity of this habitat in the future.

### ***1.3 Managing dead wood in Tasmania: a case study***

Intensive forestry in Australia is a far more recent enterprise than the timber and fuelwood harvesting that has occurred in European forests. In Tasmania, for instance, systematic silvicultural regimes have only been in place since the 1960s (Hickey and Wilkinson 1999). Prior to this, most harvesting consisted of selective logging, ('high-grading') without planned regeneration treatment (Hickey and Wilkinson 1999). Small-scale harvesting of fuelwood (i.e. the collection and

removal of timber for combustion in domestic hearths and heaters) has also been in practice for some time (Kirkpatrick 2001). Driscoll *et al.* (2000) identified over 50 vertebrate species that may be threatened by firewood collection in areas covered by Regional Forest Agreements (i.e. legislation that attempts to balance species conservation with production needs). This list would undoubtedly be much longer if invertebrates were included. While there has been no historical industrial harvesting of fuelwood in Australia, this is now planned for Tasmania's southern forests. The long-term effects of this novel, more intense, harvesting regime on dead-wood habitat are unknown (Grove 2009).

Tasmania's wet-eucalypt forests share two important features with the broadleaf and coniferous forests of Europe, the ecological importance of dead-wood resources and the old trees that give rise to those resources, and the presence of dead wood pulses that produce high volumes of dead wood about every 200-300 years (Mountford 2002). However, Tasmania's wet-eucalypt forests also differ ecologically from European forests in several key aspects. First, Tasmanian wet-eucalypt forests produce a greater volume of dead wood than do European forests (Woldendorp *et al.* 2002). This is a consequence of the potential for these forests to grow massive amounts of standing timber, coupled with slow rates of decomposition that are caused by the cool, wet climate and rot-resistant eucalypt wood (Woldendorp *et al.* 2002). Second, the dynamics of fire and the impact of fire regimes on the dead wood cycle also differ between Europe and Tasmanian forests (Thonicke *et al.* 2001). Whereas fire is a fundamental factor governing the persistence of wet-eucalypt forests, it is unimportant for the persistence of European broadleaf forests (where gap-phase dynamics rule, McCarthy 2001), and of variable importance for the persistence of European coniferous forests (Niklasson and Granström 2000). Fire does however, play an integral role for Europe's boreal conifer forests (Zackrisson 1977). Third, the structure and diversity of tree species also varies between Europe and Tasmanian forests. Dominance of one or two tree species is common in Tasmanian wet-eucalypt forest and is also the rule for boreal forests (Thomas and MacLellan 2002). However, European forests rarely reach the height of the Tasmanian wet forest eucalypts (as eucalypts are amongst the tallest flowering plant in the world and can exceed 100 m height). In contrast, most eucalypts do not live as long as many of the European boreal tree species, such as *Pinus sylvestris* and *Quercus robur*,

which can live for over 400 years (Grace and Norton 1990; Worbes and Junk 1999). Fourth, forest management in Tasmania differs from the practices employed in European forests. In Tasmanian forests, as opposed to European forests, forestry operations are still (for the most part) in the first cycle of harvesting. Hence, Tasmania's forests still retain large quantities of legacy dead wood (dead wood that is retained from the previous forest that once existed prior to conversion to plantation or disturbance such as wildfire) and a relatively intact forest landscape 'matrix'. This enables forest management to occur predominantly through coarse-filters (i.e. reserves) in combination with off-reserve management (i.e. Forest Practices Code (2000) provisions). In contrast, much of Europe has been intensively managed for timber production for centuries, producing forest stands that have, in ecological terms, lost most of their connections and resemblance to the original (or remnant) unmanaged forest. Hence, European forest management involves the micromanagement of dead-wood resources to try and aid forest recovery and to resemble a more 'natural' forest. As Tasmania's wet-eucalypt forests have not been as intensively managed and contain greater volumes of dead wood than do European forests, it should be possible to manage their dead-wood resources for more effectively than is possible in European forests. Hence, Tasmanian forest managers must assign a high priority to developing effective ways of managing and maintaining dead-wood habitat to preserve future biodiversity and forest health.

### **1.3.1 Same dead-wood thinking, different dead-wood situation**

The manner in which the forestry industry views dead-wood habitat is changing in response to the values and concerns of society (Grove and Meggs 2003). Harmon (2001) reviewed historical changes and perspectives of forest management in the USA Pacific Northwest and found that, as in other parts of the world (e.g. Europe), management strategies of dead wood habitat had progressed from 'wasteful' logging, to 'waste reduction' (which involves activities such as fuelwood harvesting and salvage logging and is also characterised as 'zero-waste tolerance'), to dead wood retention. Harmon (2001) speculated that a future progression would employ strategies to return dead-wood resources to near-natural levels. While management practices in many parts of the world are being developed to encourage the maintenance of natural levels of dead-wood, the policies of many countries are still focused solely on the retention of dead wood.

This is largely because the research needed to determine how best to manage dead wood so as to ensure that volumes return to near-natural levels, in different forest types, with different histories and climatic influences, is still lacking in many ecosystems. Although a universal set of management techniques may not be possible, with on-going research in affected parts of the world, strategies can be developed, modified and applied according to the needs of particular forest ecosystems. Grove and Meggs (2003) suggest the way forward for Tasmania's wet-eucalypt forests is to adopt an approach that involves landscape-scale modelling of dead wood in relation to forest management and natural disturbance for all silvicultural stages and setting standards for each stage. However, at present Tasmania's forest management policies (such as fuelwood harvesting in the wake of clearing and a 'zero-waste tolerance' attitude towards woody debris) still prescribe a 'wasteful logging' approach to dead-wood resources.

### **1.3.2 Wet-eucalypt forest dynamics**

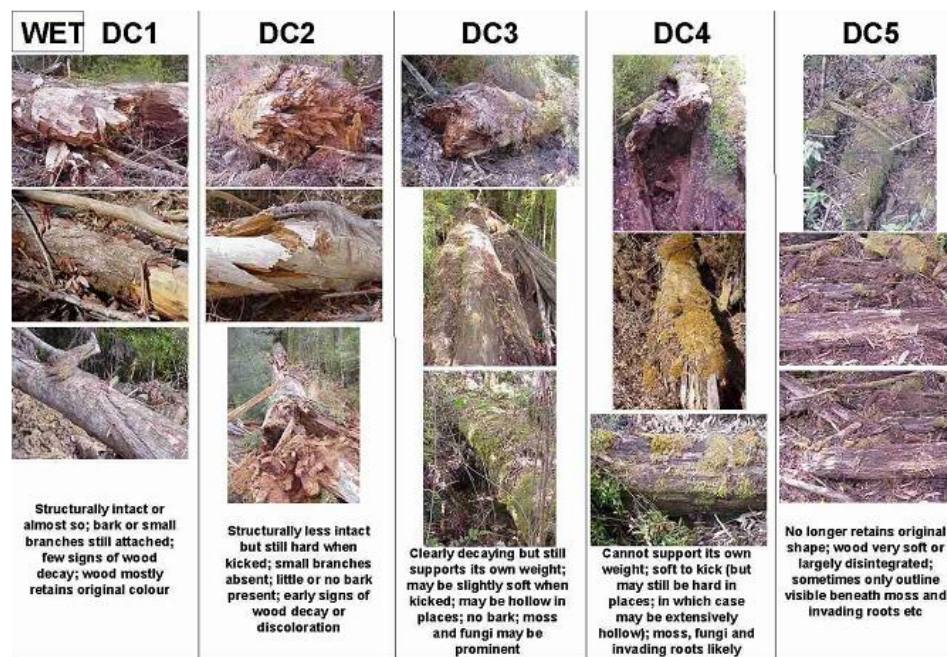
As Tasmania's forests differ from European forests, the development of useful techniques for managing dead-wood habitat in Tasmania will require a thorough understanding of the dynamics and workings of Tasmania's forests and forest industry. A typical, undisturbed, wet-eucalypt forest in Tasmania is characterised by tall eucalypts (>50 m in height), and a structurally-complex, layered forest with large amounts of litter on the forest floor. Fire plays a critical role in wet-eucalypt forests (Mount 1979; Alcorn *et al.* 2001), with the intensity and frequency of fires strongly influencing the structure of wet-eucalypt forests (Bowman *et al.* 1988; Alcorn *et al.* 2001). A high-intensity fire has the potential to kill most standing trees, much like silvicultural burns after clear-felling (though at a greater spatial scale and with less removal of biomass). In contrast, a lower-intensity fire will burn much of the understorey but leave only charring on the trunks of larger, living trees. Hence, a forest stand can be comprised of several different age-classes, depending on the intensity of past fires and the success of subsequent regeneration events. Where there is high rainfall and long fire-intervals, wet-eucalypt forests compete with rainforest ecosystems for site occupation (Webb 1968).

As fire is so dominant in wet-eucalypt forests it is thought to be the main driver of dead wood production. Indeed, volumes of dead wood are high in these forests



because of the preponderance of dead, fire-killed trees that produce large-diameter logs, which are slow to decompose (Woldendorp *et al.* 2002; Grove and Meggs 2003; Grove *et al.* 2009). However, depending on the biomass of the living stand and the forest age, the volume of dead wood created by fire can vary, or even be destroyed completely. In addition, dead wood is not necessarily created synchronously with the fire event, as branches can be weakened by fire and fall at any stage. Indeed, there can be a long lag time between the production of standing timber and its appearance on the forest floor as dead wood. Moreover, as in European forests, factors such as disease and wind will also introduce dead wood to the forest floor and mediate the extent of heterogeneity in this resource.

As woody debris breaks down it passes through various stages of decay. Initially the wood is solid and in some instances remains structurally intact and retains bark, but by later stages of decay it becomes devoid of structure (Yee *et al.* 2001). Figure 1.1 illustrates the decomposition of logs in wet-eucalypt forests and the five decay-class system that is used by researchers to categorise dead wood in Tasmanian wet-eucalypt forests (Yee 2005; Stamm 2006). The log decay-class system is proven to capture the ecology of decomposition in some eucalypts (Grove *et al.* 2011); however, Gates (2009) revealed ambiguities associated with classifying decay stages this way for biological use (Grove *et al.* 2011) i.e. for surveying fungi associated with decay stage. To overcome these ambiguities Gates (2009) developed a nine decay-class system to capture intermediate stages of decay. The nine decay-class system was applied to the current study because it was useful in accommodating different wood species (i.e. non eucalypt species) and for better capturing the associations between decay stage and the study species. This new decay class system should address problems with the unevenness of the interval between decay classes like those found in Gates (2009). The nine decay-class system is explained in Chapter 5.



**Figure 1.1** An extract from field surveying sheets used for decay classification of eucalypt logs in wet-eucalypt forest, based on five decay classes (DC) (after Grove *et al.* 2009).

### 1.3.3 Forestry practices in Tasmania's wet-eucalypt forests

Clearfelling, high-intensity burning and aerial sowing (CBS) has been the standard silvicultural system for lowland wet-eucalypt forests in Tasmania since the 1960s (Hickey and Wilkinson 1999). The clearfell, burn and sow system is the result of research from a study conducted by Gilbert (1958) demonstrating that CBS built on the forest's natural relationship with fire. Studies since have revealed that CBS is very efficient in ensuring the regeneration of eucalypts (Hickey and Wilkinson 1999; Elliot *et al.* 2008).

Nevertheless, CBS greatly simplifies the forest structure and initiates a decline in the abundance and heterogeneity of dead wood. As the rotation length of forests following a CBS harvesting regime is short (notionally 80 years), successive silvicultural cycles will limit the subsequent recruitment of dead wood (Grove 2002b; Yee 2005; Forestry Tasmania 2009; Grove *et al.* 2011). Hence, CBS does not allow for the creation of late-successional forest structure (Hickey *et al.* 2001), such as large-diameter logs (Hickey and Saava 1992; Meggs and Taylor 1999; Grove 2002b). Studies also suggest that the diversity of vascular plant species in both the understorey and overstorey is also reduced following CBS (e.g. *Gahnia grandis* and *Pteridium esculentum* invasion following CBS; Hickey 1994; Turner 2003).

### 1.3.4 Biogeography and dead-wood habitat

Unlike most of northern Europe, southern Australia did not experience extreme glaciation during the last Ice Age (Harland and Herod 1975). Throughout the Quaternary, however, climatic variability at a localised level did affect the vegetation, and although many forest types would have been geographically restricted, they managed to persist (Kirkpatrick and Fowler 1998). Forests in many parts of southeastern Australia, including Tasmania, show evidence of recent expansion from glacial refugia (Byrne 2008) and many of today's species of flora and fauna would have been able to survive through the last glacial cycle by finding refuges from the harsh conditions. Indeed, these refugia are important areas of local endemism, where species with poor dispersal ability or specialised habitat requirements have persisted (Harvey 2002). These traits, which are characteristic of saproxylic beetles, may explain the patchy distribution of some southern species (e.g. the threatened stag beetle, *Lissotes menalcas*, Chapter 6).

Poor dispersal ability among saproxylic species is expected for two reasons: under the natural condition the beetles have adapted to dead wood is abundant and slow to decompose, particularly in wet-eucalypt forests (Stamm 2006; Grove *et al.* 2009), such that there might be little motivation or need to disperse.

Consequently, dead-wood-dependent species have had no need to develop long-distance dispersal mechanisms. This implies that saproxylic species will not easily or rapidly recolonise a site following a local decrease in dead wood, such as that caused by wildfire or timber harvesting (Meggs 1996; Schiegg 2000; Grove and Meggs 2003).

Tasmania's varied topography and steep rainfall gradients may also explain the restricted ranges of many of the island State's native species, including the saproxylic beetles. Mesibov (1994) identified a number of discontinuities in species-ranges, termed faunal breaks, on the main island of Tasmania. The ecotones that separate these faunal breaks reflect a complex relationship between geology, topography and rainfall gradient, and these factors create a dispersal barrier (Mesibov 1994) or otherwise influence distribution (Meggs *et al.* 2003). Meggs *et al.* (2003) describe the distribution of three species of *Hoplogonus* (Coleoptera: Lucanidae) that occupy a small area in the north-east of Tasmania; there is virtually no overlap of the species' ranges even though they occur in the same region. The presence of a granite batholith in this region (Groves 1977;

McCarthy and Groves 1979) may be responsible for the restricted distribution of these species by acting as a barrier for dispersal. The roles that geology, aspect, temperature and altitude play in determining species distributions and influencing community composition remain largely unexplored in Tasmania, though one study has provided an initial model of biogeographical regions for the state (Peters and Thackway 1998).

### **1.3.5 Thesis structure and objectives**

This study aims to provide an understanding of the ecology and habitat requirements of Tasmania's saproxylic beetles, to facilitate the development of effective management strategies that ensure their long-term persistence in the landscape and to avoid the impact of threatening processes that elsewhere (particularly in Europe) have resulted in the decline or extinction of many populations of saproxylic beetles. Describing the life-history strategies, diet requirements, and habitat preferences (essential dead-wood characteristics) of this group of invertebrates can provide the necessary data with which to formulate management plans and predict how a particular species will react to pressures of loss of dead-wood habitat and fragmentation of landscapes.

Yee (2005) found over a hundred species of saproxylic beetles in large- and small-diameter *Eucalyptus obliqua* logs in Tasmanian wet-eucalypt forest, the majority of which were rare (infrequently detected). This study aims to characterise the ecology and life-history characteristics of six Tasmanian saproxylic beetle species (that are thought to differ in their sensitivity to changes in dynamics of dead wood), belonging to the families Cerambycidae, Tenebrionidae, Curculionidae, Prostomidae and Lucanidae (Yee 2005). In addition, the study aims to describe the ecology and life-history characteristics of the threatened Tasmanian stag beetle, *Lissotes menalcas*, because it has been identified by Forestry Tasmania as a species requiring urgent research; research that aims to improve management practices of species dependent on dead wood. All six species are known to live inside dead wood for a large part of their life cycle and are thought to gain their nourishment from the decaying wood. The close relatives of some of these species are vulnerable to extinction in Europe e.g. *Prostomis mandibularis* and *Lucanus cervus*,

The overall objectives of this study are (1) to increase our (currently poor) understanding of the ecology and dynamics of saproxylic beetles in Australian forest ecosystems, with particular emphasis on species found in cool-temperate wet-eucalypt forests of Southern Tasmania; (2) to determine to what extent characteristics of dead wood at the log, site- and landscape-scale explain the presence or absence of selected saproxylic beetles; (3) to understand the role that forest management history plays in shaping the dead wood substrate; and (4) to use the information on species ecology gained in this study to propose management recommendations for these beetles in the production forests of Tasmania. The thesis addresses each of these objectives in turn, beginning with investigation of the ecology and ecological requirements of the study species (Chapter 3 and 4), continuing with a multi-scale modelling approach that links environmental parameters at varying spatial scales to the occurrence of each of the study species (Chapter 5 and 6), and culminating with a detailed discussion of the implications of these findings for the conservation and management of these species in Tasmania's forests.

### **1.3.6 Detailed overview of data chapters and synthesis**

Chapter 3: *Sexual Development of sympatric Tasmanian saproxylic beetles (Lucanidae, Coleoptera)*

Insects are confronted with a range of varying physical and biotic factors that change according to seasons and have therefore evolved different life-history adaptations in order to survive (e.g. variable growth rates, differing numbers of generations, dormancy, longevity, a synchronised reproductive period with environmental conditions, and variable fecundity and longevity rates; Cardenas and Hidalgo 2000). It is important to characterise these life-history traits to understand the ability of beetles to persist in the face of threatening processes, such as the reduction of dead wood in the landscape. Such information will also assist in predicting the propensity for these saproxylic beetles to increase their populations or colonise new habitat, after perturbations. The life-history of most saproxylic beetles remains poorly known and very few studies have examined how life-history traits vary in relation to environmental factors, and specifically in relation to dead-wood resources. Indeed, the majority of studies of the life-history of saproxylic beetles to date have investigated just one factor of their ecology, such as fecundity (Jonsson 2003; Holland *et al.* 2005), or resource allocation and

trade-offs (Jonsson 2003), and ubiquitously call for more research on the ecology of this group of species (Michaels 2000; Grove 2006). This study uses a simple score-based assessment of the reproductive features of both sexes to identify sequential stages of sexual development. Subsequently, inferences are made about the difference in the apparent abundance of the two species and the implications of this for their conservation are discussed.

*Chapter 4: Can molecular techniques untangle the feeding relationship between a mycophagous beetle and its putative food-source? A preliminary study on the Tasmanian saproxylic beetle Prostomis atkinsoni (Coleoptera, Prostomidae)*

Diet is fundamental to all organisms, as it directly influences the fitness of an individual and its ability to complete its life cycle. As saproxylic beetles physically inhabit their food resource they must choose dead wood that fulfils their dietary requirements. Their preferences for dead wood are therefore likely to depend on the presence (or absence) of specific micro-organisms in the wood (e.g. wood-rotting fungi; Tanahashi *et al.* 2009).

This chapter takes the first step towards establishing mycophagy in a Tasmanian saproxylic beetle by applying molecular techniques to isolate fungi from a rotten-wood type potentially available as food, and from the guts of the beetles. If successful, this may allow the fungal assemblages to be correlated, enabling some tentative inferences regarding mycophagy to be drawn and further hypotheses to be raised.

*Prostomis atkinsoni* is thought to be an ideal simple model species with which to address this aim as it is found almost exclusively in one rotten-wood type from two species of eucalypt ('gingerbread rot' in *Eucalyptus regnans* and *E. obliqua* species).

*Chapter 5: Relationship between the attributes of coarse woody debris and the presence/absence of selected saproxylic beetle species*

Landscape processes and the local spectrum of dead wood substrate can both influence the presence and abundance of saproxylic beetles. This chapter aims to understand the role of CWD characteristics in determining the presence or absence of saproxylic species at the immediate CWD-scale (where beetles reside) in order to obtain information that can assist in the development of improved local-scale management strategies for the conservation of saproxylic beetles. The

specific aims of this chapter are: (1) identify specific microhabitat (rotten wood types) requirements of six saproxylic beetles within wet-eucalypt production forest in Tasmania, (2) identify specific CWD habitat requirements of six saproxylic beetles within wet-eucalypt production forest in Tasmania; and (3) determine whether CWD-scale environmental variables can predict the presence of these species in this environment.

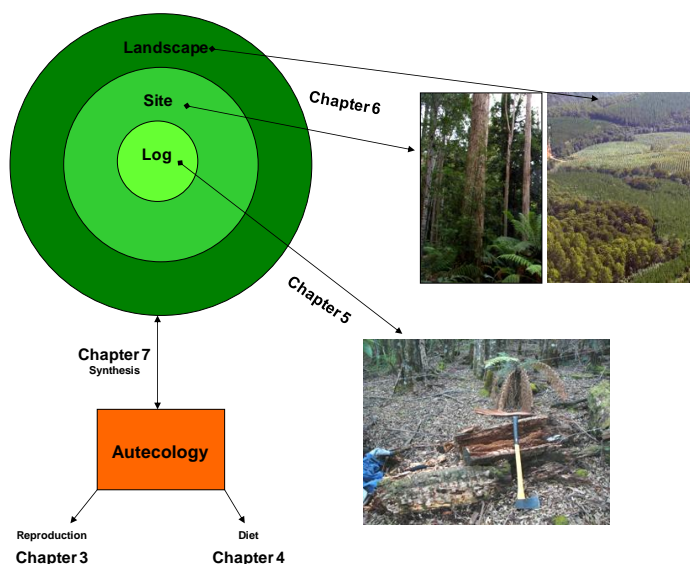
*Chapter 6: The influence of site and landscape variables on the presence of saproxylic beetles in wet sclerophyll forest*

Scaling up from the Chapter 5, this chapter aims to understand the role of site and landscape variables in determining the presence or absence of saproxylic species at broader spatial scales in order to obtain information that can assist in the development of improved broad-scale management strategies for the conservation of saproxylic beetles. The specific aims of this chapter are (1) identify specific site and landscape habitat requirements of six saproxylic beetles within wet-eucalypt production forest in Tasmania, (2) determine whether site- and landscape-scale environmental variables can predict the presence/absence of these species in this environment (3) establish whether site- and landscape-scale variables can robustly predict the presence/absence of saproxylic beetles in the environment and thus, alleviate the necessity to conduct intensive, on-ground surveys to characterise fine-scale habitat features (cf. rotten wood types, Chapter 5); and (4) discuss implications of the findings of this study for the management of Tasmania's threatened stag beetle, *Lissotes menalcas*.

The aim of separating Chapter 5 and 6 is to assess what predictions can be made when only data from one particular scale was used, and to determine which scale is best for predicting the occurrence of saproxylic beetles in this forest ecosystem. In addition, the intention is to determine what types of data are required to make adequate predictions of species occurrence at multiple scales (assuming that not all data can be collected at all scales). By separating the chapters the following questions can be answered: do the best predictor variables for developing predictive habitat models come from GIS information at the landscape-scale, or from using site-scale information such as the forest classification system (FC), or is it the finest scale (CWD-scale) where logs are physically cut open, that provides the best predictor variables to successfully model presence/absence of the study species? This is a likely scenario in real forestry work where tools such as GIS,

This chapter discusses how the findings of the complementary studies that make up this thesis (Chapter 3 to 6) can be applied in future research, modelling and management. In particular, this chapter utilises the novel information gained throughout this thesis to make management recommendations for the conservation of the study species in Tasmania's wet-eucalypt forests and for conserving saproxylic species more widely.

To complement the written description of the thesis structure a conceptual diagram is presented below (Figure 1.2).



**Figure 1.2 A conceptual model that illustrates the thesis structure.**



## 1.4 References

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## CHAPTER 2 DETAILS OF STUDY AREA AND SPECIES

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Chapter 2 provides an overview of the study area, the management history, the processes that are acting upon the landscape of this area, and the study species that inhabit it. Providing details of the study area and the study species sets the scene for the conditions under which the study was undertaken and is an integral part of the framework developed to meet the study aims outlined at the end of Chapter 1, but greater detail is provided in later chapters where necessary.

The study area was chosen for four reasons: (1) all the study species are known to occur in this area and therefore the area could be sampled with the chance of finding each of the study species, (2) environmental features such as geology, fire history and vegetation types are all known and well documented for this area and are variables previous studies have found to be important for predicting species presence or absence (see Chapter 5 and 6 for more detail), (3) these environmental features are likely to influence the distribution of CWD and saproxylic beetles as will be considered later in the thesis in terms of specific testable hypotheses; and (4) the study area has a varied, traceable forest management history, which is important for elucidating forestry activities that favour or adversely affect the persistence of saproxylic beetle populations - knowledge that becomes important for explaining species presence/absence in Chapter 5 and 6.

### 2.1 Description of study area and its forest types

#### 2.1.1 Location

The study area was located in the southern wet-eucalypt forests of Tasmania. These forests lie west of the town of Geeveston (43°04' S, 146° 41" E), which is a 1.5 hour drive from, Hobart. The entire study was conducted in State forest which is owned and managed by Forestry Tasmania. A map of the area (approximately 13 x 30 km) is provided in Appendix 2.1.

The study area ranges in elevation from 60 to 200 m above sea level and is surrounded by topography ranging from valley bottoms at 30 m to 1338 m above sea level. Mountain ranges surround three sides of the study area: Mt Weld in the north-west which is the highest, reaching 1338 m, Mt Picton (1328 m) in the south-west and the Hartz Mountains (1255 m) in the south (Yee 2005).

### 2.1.2 Environmental features of the study area

#### *Climate*

The study area experiences a temperate maritime climate dominated by westerly weather systems. The mean annual rainfall of 1477 mm is fairly uniform in its distribution throughout the year but slightly higher rainfall occurs from winter through to spring (Bureau of Meteorology) and strong westerly winds are common in spring. Long-term weather averages show a mean minimum annual temperature of 6.3 °C and a maximum mean annual of temperature of 17°C (Bureau of Meteorology, Warra LTER weather station). During winter, temperatures can fall below 0 °C and in summer temperatures can exceed 30 °C.

#### *Geology and soils*

The dominant rock type in the study area is Jurassic dolerite, a basic igneous rock which yields moderately fertile soils on weathering. Two other rock types also underlie parts of the area: Permian mudstone and Pre-Cambrian quartzite sandstone, both of which yield nutrient-poor weathering products. The dominant soil types in the study area are those derived from the dolerite (Laffan 2001). Soils derived from Quaternary slope deposits also feature throughout the study area (Woldendorp *et al.* 2004).

#### *Vegetation and fire history*

The forests of the study area are classed as wet eucalypt (Harris and Kitchener 2005) , a forest type that is well represented in Tasmania's native forest (approximately 883 000 ha) (Forestry Tasmania 1998). The wet-eucalypt forests fall into two categories: wet sclerophyll and mixed forest, both of which are tall forests with an overstorey of one or more species of eucalypt. The dominant eucalypt species in the study area are *Eucalyptus regnans* and *E. obliqua* and the CWD of these species dominates the forest floor (Woldendorp *et al.* 2002). Wet-eucalypt forests contain a dense understorey comprised of broad-leaved shrubs as well as ferns. In the mixed forests the understorey is dominated by several rainforest species (Kirkpatrick *et al.* 1988). The floristics of the understorey species varies due to local fire history, soil fertility and aspect (Mount 1979). In some parts of the study area, fertile dolerite soils combined with high rainfall produce wet-eucalypt forests with great productivity (volume of standing timber); whereas in other parts of the study area, less-fertile soils derived from mudstone and quartzite produce less productive forests. In addition to this, north-facing

slopes are more sun-exposed and generally support drier forest, unlike south-facing slopes where mixed forests dominate. A more detailed discussion of the vegetation communities in the study area and the influence of fire, aspect and geology can be found in Harris and Kitchener (2005); and in the surrounding area by Corbett and Balmer (2001). The interplay between fire, aspect and geology of how and how they influence forest type is discussed in Chapter 6.

Wildfire is the natural disturbance process that allows or triggers the regeneration of Tasmanian wet-eucalypt forests. If fire is absent from these forests for more than 350 years the eucalypt overstorey gradually dies out and the rainforest trees assume dominance (Gilbert 1958; Mount 1979). High-intensity wildfires can result in complete mortality of overstorey eucalypts, while lower-intensity fires allow for some tree survival resulting in multi-aged stands.

The fire history of the study area has been well documented. This area was subject to major wildfires in 1898, 1934 and 1966/1967. Some were of sufficient intensity to be considered stand-replacing, but most were lower-intensity fires, and many of today's standing old-growth trees have survived one or more of these fires (Dick Chuter, personal communication; Turner *et al.* 2009). Some parts of the study area have been subject to more than one major wildfire, resulting in two or more age cohorts (personal observation). During the early 1900s some of these sites were subject to multiple burning by hunters and tree harvesters (Elliot *et al.* 2008)

### **2.1.3 Management history of the study area**

Sites chosen for sampling fall into one of three categories of management history: regrowth, logged and old-growth.

#### *Regrowth (eucalypt growth from natural disturbance)*

Much of the regrowth in this area is a product of the 1934 and 1967 wildfires, although it is important to acknowledge that selective logging occurred throughout the area during this time (Hickey *et al.* 1999). The sampling sites that are categorised as regrowth forest look structurally similar to those with forest regeneration (eucalypt regeneration after logging) from the 1960s; the overstorey and understorey species have similar canopy coverage, heights and dominant tree and shrub species. However, these regrowth forests are liable to support more

large eucalypts, higher volumes of CWD and a denser understorey. These features are characteristic of, but not exclusive to, regrowth sites.

### *Harvested*

The study area has been subject to timber harvesting for over a century and it is a small part of an area that is now an actively managed, large-scale industrial timber harvesting region. Clearfell burn and sow (CBS) is the main management technique, whereby all merchantable trees from a designated area (coupe) are harvested in one single operation. The remaining debris is ignited to create a receptive seedbed, followed by aerial sowing of local eucalypt seed for regeneration (Hickey and Savva 1992). Sites within the study area cover a range of regeneration ages from 20 to 60 years. Therefore some of these sites have undergone the CBS regime whilst others have been selectively harvested. The majority of regenerating CBS harvested coupes in this area are approximately 30 years old (Yee 2005); however, selective harvesting occurred in parts of the study area prior to 1960.

### *Old-growth*

Old-growth forest within the study area was identified using the nationally agreed definition: “ecologically mature forests where the effects of disturbance are now negligible” (*National Forest Policy* 1992; Forestry Tasmania 2004). Whilst the definition can allow for some history of selective logging, the old-growth sites used in this study had no evidence of this. Old-growth forests in this study area contain many large-diameter living trees, large-diameter CWD and rainforest species, despite showing signs of being partly burnt in the 1898 and/or 1934 wildfires.

The management-history categories described above can be further categorised into six broad forest types, with two sub-categories included in the eucalypt regeneration from harvesting. This category was split into two treatments to reflect the change (to the pulp and timber markets) in forest management practices over time. These six categories explain the management histories of each site, and are explained in more detail in the section that follows.

### 2.1.4 Study Sites

Six broad forest types were identified and chosen for this study. These broad forest types are classified by Forestry Tasmania and are described as follows:

- Mature eucalypt forest without regrowth ('old-growth')
- Mature eucalypt forest with regrowth tree height not measured ('old-growth with regrowth')
- Mature eucalypt with regeneration of known age ('harvested')
- Unaged regrowth eucalypt with mature eucalypt element ('regrowth')
- Pure unaged regrowth eucalypt ('regrowth')
- Eucalypt regeneration arising following harvesting
  - (a) Eucalypt regeneration 1967-1979 ('harvested')
  - (b) Eucalypt regeneration 1980-1999 ('harvested').

A number of forest types form sub-categories under the six broad forest classes and they are called 'forest classes' (Forest Class System (FC), Forestry Tasmania 2005). The FC system is used to stratify forest types into classes which have broadly similar timber volumes and structural characteristics. These 'forest classes' are therefore useful for timber inventory and harvest planning. In this case, the FC system was used to identify sites based on the land use history as described in Section 2.1.3 of this chapter. The FC system is discussed in detail in Chapter 5 where it is used as a predictor variable for the development of predictive habitat models.

Two hundred randomly stratified sites were generated according to the six broad forest types described above. The 200 sites were then plotted on a map of the study area (Appendix 2.1). Sites were considered to be suitable to sample after some deliberation over maps of the study area, discussion with others more familiar with the area and many field visits. Five replicates were selected for each treatment - a total of 35 sites (Table 2.1). The 35 sites were chosen because they represented the most common and easily accessible forest classes (sub-categories of the six broad forest type 'treatments' described above).

Each site met the following criteria: no more than 1 km from a road and no less than 40 m from a road; within the range of the threatened stag beetle *Lissotes*



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*menalcas* (Lucanidae); comprised of lowland wet-eucalypt forest (altitude <350m); and relatively flat (sloping at <15°). All study sites had similar elevation, slope and aspect was north- or south-facing. There was approximately 30 km between the two most distant sites, and some sites were separated by the Arve or Huon River (Appendix 2.1).

**Table 2.1 Location of study sites including aspect and broad forest type defined by the FC 2001 system (continued next page).**

Site	General area	Broad forest type (treatment)	GDA eastings	GDA northings	Aspect
138	Arve Loop Road	Mature eucalypt forest without regrowth	480300	5224215	South
134	Bermuda Road	Mature eucalypt forest without regrowth	491900	5232250	South
51	Arve Spur 2	Mature eucalypt forest without regrowth	478850	5227050	South
36	Arve Loop Road	Mature eucalypt forest without regrowth	479825	5225300	South
135	Arve Spur 3/2	Mature eucalypt forest without regrowth	483650	5223650	South
12	Arve Road Opp Spur 1	Mature eucalypt forest with unheighted regrowth	479550	5228255	North
13	Arve Rd nr Spur 1	Mature eucalypt forest with unheighted regrowth	478625	5227650	South
2	Edwards Link Road	Mature eucalypt forest with unheighted regrowth	480700	5231525	North
145	Bracken Ridge Trail	Mature eucalypt forest with unheighted regrowth	486725	5232325	South
167	Edwards Link Road	Mature eucalypt forest with unheighted regrowth	485500	5232150	South
18	Edwards Rd (1km from turnoff)	Mature eucalypt with aged regeneration	483525	5225900	South
3	Southwood Spur 5	Mature eucalypt with aged regeneration	488125	5225150	North
104	Cnr of Edwards and Arve Road	Mature eucalypt with aged regeneration	482500	5226050	South
120	Arve Spur 1	Mature eucalypt with aged regeneration	480500	5228850	South
9	Edwards Rd nr Spur 4	Mature eucalypt with aged regeneration	483350	5231150	North
58	Fletchers Road	Unaged regrowth eucalypt with mature	477800	5233300	North
4	New Road Sp 2	Unaged regrowth eucalypt with mature	496125	5231150	South
24	Arve Rd	Unaged regrowth eucalypt with mature	478550	5227825	North
25	Southwood Road nr Bridge	Unaged regrowth eucalypt with mature	484975	5233000	South
146	Eddy Road	Unaged regrowth eucalypt with mature	479975	5234350	North
37	Lethbridge Sp 4	Pure unaged regrowth eucalypt	492100	5232000	North
191	Lethbridge Sp 3	Pure unaged regrowth eucalypt	494125	5232150	North
79	Southwood Rd	Pure unaged regrowth eucalypt	487450	5230900	South

Site	General area	Broad forest type (treatment)	GDA eastings	GDA northings	Aspect
125	Arve Sp 3	Pure unaged regrowth eucalypt	483925	5224450	North
17	Ligerwood Road	Pure unaged regrowth eucalypt	490500	5229535	North
90	Peppers Rd	Eucalypt regeneration 1960-1979	485850	5226500	South
91	Southwood Road	Eucalypt regeneration 1960-1979	486800	5227725	South
136	Ligerwood Road	Eucalypt regeneration 1960-1979	488350	5225900	South
134	Southwood Road nr Ligerwood Sp 2	Eucalypt regeneration 1960-1979	486700	5227425	North
127	Ligerwood Road	Eucalypt regeneration 1960-1979	490000	5228250	South
22	South Weld Road	Eucalypt regeneration 1980-1999	478150	5231450	South
62	East Picton Spur 4	Eucalypt regeneration 1980-1999	478000	5227350	North
186	Riveaux Rd Sp 1	Eucalypt regeneration 1980-1999	474150	5227100	South
114	Edwards Road	Eucalypt regeneration 1980-1999	479750	5231525	North
99	Conways Road	Eucalypt regeneration 1980-1999	485250	5225250	South

## 2.2 Study species

The purpose of this section is to present all the current information that is available for each species. The information here has been acquired from literature, from specialists, and from field observations made during this study; the level of detail therefore varies among species.

References for the original taxonomic description have been provided after the species name for all species except *Dryophthorus* ECZ sp. 02, because it is undescribed.

The six saproxylic beetles chosen for this study met the following criteria:

- they are all found in sufficient numbers to obtain reasonable sample sizes
- they all occur in wet-eucalypt forest
- they all occur in CWD and are thought to be gaining nourishment from the rotten wood.
- adults and larvae could be found inside the log

It is recognised that a selective sampling technique has been used in this study and that other techniques would have delivered different results biasing the sampling of different species e.g. flight intercept traps. The species in this study are thought to spend more than one year inside the log so the chance of locating them is increased when directly cutting into the log, unlike sampling using flight intercept traps or pitfall traps where species are often only in flight or mobile during the spring/summer period. Inside the log, each species occurred separately in small groups as adults and larvae, making it relatively easy to sample both life stages; however, *Toxentes arcuatus* and *Coripera deplanata* adults and larvae were found separately.

The six species chosen here represent both common and less common saproxylic beetles from this region in Tasmania. Some of them are widespread throughout Tasmania e.g. *C. deplanata* and *T. arcuatus*, some of them are flighted and some are not but they are all considered to be representative of obligate saproxylic beetles, spending a part of their life cycle inside logs. In addition to this, the taxa

in this study are likely to be representative of a subset of saproxylic species that might be expected to be most impacted by forestry i.e. they are not highly mobile, nor are they early successional saproxylic species or species utilising fine woody debris.

Distribution maps for each species can be found on the Tasmanian Forest Insect Collection (TFIC) website: [www.tfic.net.au](http://www.tfic.net.au). These distribution maps were developed from location information of the specimens housed in the TFIC, Forestry Tasmania, Hobart.

### 2.2.1 *Lissotes menalcas* Westwood, 1855 (Lucanidae: Lucaninae)

There are twenty-eight species of the genus *Lissotes* known in Australia and twenty-two are endemic to Tasmania. One of the endemic species found in Tasmania is *Lissotes menalcas*, a large, black, flightless beetle (Figure 2.1). The males have large mandibles and a body length ranging from 16 to 25 mm (Meggs and Taylor 1999). It is easy to distinguish from other *Lissotes* species because it has a highly polished exoskeleton; its prothorax is peaked in appearance and the head is largely excavated (Lea 1910). Females have a polished exoskeleton that is duller in appearance due to large, dense punctures on the head and prothorax. The females are slightly smaller than the males; their body length varies between 12 and 20 mm. Lucanid larvae are easily recognisable by their ‘c-shape’ and by their heavily chitinated head capsule (Figure 2.1). It is not possible to distinguish between the larvae of *L. menalcas* and *L. cancroides* (the other lucanid species included in this study) with the naked eye, although *L. menalcas* larvae reach a larger size (personal observation).



Figure 2.1 Left: *Lissotes menalcas* adult male extracted from rotten wood of *Eucalyptus regnans*; right: *Lissotes menalcas* larva situated in rotting wood of *Eucalyptus obliqua*.

*Lissotes menalcas* occurs in south-eastern Tasmania only. Its total range is approximately 3050 km<sup>2</sup> (Grove *et al.* 2002). Included in this range are the southern forests, parts of the Wellington Range, South Bruny Island and the Tasman and Forestier Peninsulas.

*Lissotes menalcas* is found in a broad range of wet forest communities, ranging from old-growth mixed forest to twenty-three-year-old wet silvicultural regeneration (Meggs and Taylor 1999). *Lissotes menalcas* is found predominantly in CWD from eucalypt trees, but has also been recorded in logs of rainforest species (Meggs and Taylor 1999). *Lissotes menalcas* is thought to occur exclusively in CWD with a diameter greater than 5 cm (Karen Richards, personal communication; personal observation). It has not been found at altitudes greater than 650 m, nor where annual rainfall is below 700 mm.

Until recently, *Lissotes menalcas* was classified as vulnerable under the Tasmanian *Threatened Species Protection Act 1995* (TSPA 1995) because it was predicted the species would undergo a population loss of 20% in the following 10 years due to habitat loss (Criterion A2). Because new records have led to the recognition of a larger range the species qualified for downgrading of its vulnerable status and is now classified as rare. Due to its restricted habitat range and to the nature of threatening processes (e.g. silviculture) the species is identified as a Category 3 fauna species (those species whose conservation needs to be met by management prescriptions) under the Tasmanian Comprehensive Regional Assessment process (*Tasmanian Public Land Use Commission* 1997). It has also been identified as a Priority Species ‘requiring recovery action’ under the Threatened Species Section (2012) *Threatened Tasmanian Stag Beetles Recovery Plan*, Department of Primary Industries, Parks, Water & Environment, Hobart and the *Tasmanian Regional Forest Agreement* (Part A.1) signed between the Commonwealth of Australia and the State of Tasmania in November 1997.

### **2.2.2 *Lissotes cancroides* Fabricius, 1787 (Lucanidae: Lucaninae)**

*Lissotes cancroides* is a small, dull black flightless beetle, endemic to Tasmania (Figure 2.2). The shape of its mandibles and slightly peaked prothorax distinguish it from the other Tasmanian *Lissotes* species. Its exoskeleton is coated with setae which give it a greyish appearance. Male body length varies between 12 and 20 mm and females are between 10 and 16 mm.



**Figure 2.2** Adult male *Lissotes cancroides*.

Its exact distribution is currently not known; however, it is widespread in wet sclerophyll, mixed forests of lowland southern Tasmania and has been found at altitudes over 650 m (personal observation). The species has not been recorded elsewhere in Tasmania despite intensive searching on the north-west, north-east and east coasts (personal observation).

*Lissotes cancroides* tended to be more readily encountered in the study-area than its Threatened relative *L. menalcas*. It is generally accepted that *L. cancroides* more widespread than *L. menalcas* and more common within its known range.

### **2.2.3 *Prostomis atkinsoni* Waterhouse, 1877 (Prostomidae)**

*Prostomis atkinsoni* is an endemic Tasmanian beetle (Figure 2.3). Currently five species of the genus *Prostomis* are known in Australia (Schawaller, 1993), three of which occur in Tasmania. Adult *P. atkinsoni* have a copper-coloured, dorso-ventrally flattened body, and are distinguished by the shape of the jugular processes protruding anteriorly from the thorax (Schawaller 1993). There are morphological differences between males and females. Males have a body length between 8 and 10 mm, while females are between 6 and 9 mm long.



**Figure 2.3 Left: adult *Prostomis atkinsoni*; right: larva of *Prostomis atkinsoni*.**

Adult *P. atkinsoni* have well-developed wings and are occasionally observed in flight in warm weather (Simon Grove, personal communication).

The full distribution of *P. atkinsoni* is currently not known, although it is readily found in the wet-eucalypt forest of southern Tasmania and it has also been recorded on the east coast of Tasmania and near Cradle Mountain (Simon Grove, personal communication).

#### **2.2.4 *Dryophthorus* ECZ sp. 02, undescribed (Curculionidae: Rhynchaeninae)**

*Dryophthorus* ECZ sp. 02 is an undescribed weevil (Figure 2.4) as indicated by its current name (ECZ are the initials for E.C. Zimmerman, an expert on Australian Curculionidae). Its habits, size and colour make it very cryptic. It is a very small (approximately 3–4 mm in length), grey-brown weevil that inhabits the rotten wood of *Eucalyptus* logs and is often embedded in and camouflaged by damp muddy or fibrous rotten wood. The genus *Dryophthorus* occurs in Africa, Asia and Europe. One species *D. corticalis* is considered vulnerable to extinction in the United Kingdom (Alexander 1995).

The species spends most of its life cycle inside logs but has been caught in pitfall traps, which suggests that it can disperse when new habitat is required or to look for mates. There is no further information regarding the species' life-history attributes.





**Figure 2.4** *Dryophthorus* ECZ sp. 02.

This species is currently only known to occur in the southern wet-eucalypt forests, though this may reflect the lack of intensive searching elsewhere in Tasmania where potential habitat exists. One study by Yee 2005 found that *Dryophthorus* ECZ sp 02 prefers large-diameter CWD comprised of a brown, wet rotten-wood type (Yee 2005).

#### **2.2.5 *Coripera deplanata* Boisduval, 1835 (Tenebrionidae: Adeliinae)**

*Coripera deplanata* is a dark brown/black, flightless beetle (Figure 2.5). It is endemic to Tasmania and was originally described as *Adelium deplanatum* but later moved to the genus *Coripera* (Matthews 1998). It can be distinguished from other similar beetles by the form of antenna and mouthparts, and by its uniquely sculptured exoskeleton (Figure 2.5; Tillyard 1926). There is no noticeable size difference between males and females; they are both approximately 3 cm in length. The larvae (Figure 2.5, right) are easy to recognise—they have an elongate, cylindrical body with two protrusions extending from the posterior, and the antennae are short and clubbed.



**Figure 2.5** Left: Adult *C. deplanata*, right: *C. deplanata* larva.

Specimens of *C. deplanata* have been found in wet sclerophyll and mixed forests state-wide.

### 2.2.6 *Toxotes arcuatus* Fabricius, 1775 (Cerambycidae: Prioninae)

*Toxotes arcuatus* is widespread throughout the state and is not endemic to Tasmania, occurring also in the southern parts of mainland Australia. This longhorn beetle is easily recognisable by its large size and by the great length of its many-jointed antennae (Figure 2.6, left). The body is copper in colour, and adults can reach 6cm in length. The larvae are elongate and legless and have short, stout jaws embedded well into the head. The thoracic segments are broader than the abdominal segments, which are slightly corrugated, flattened on the dorsal and ventral surface, and broadly rounded at the anal extremity (Froggatt 1923).



**Figure 2.6 Left: Adult *Toxotes arcuatus*; right: *T. arcuatus* larva.**

The larvae hatch during February/March and immediately start boring into the wood of the host log; they are similar in form to the final instar (Froggatt 1923). They feed the under surface of the bark and in the upper layers of the sapwood making regular-shaped tunnels, feeding as they tunnel ahead and packing sawdust and frass behind them (Froggatt 1923). Once the larvae reach their final instar they cut a shaft through the sapwood and, after feeding in the deeper wood for a short time, pupate in the solid wood several centimetres beneath the outer surface (Froggatt 1923). They are in the pupal stage from October through to December, with adults emerging during summer (personal observation).

The larvae have been reared from *E. regnans* logs, emerging in years six and seven; they could potentially take nine years to complete their life cycle (Dick Bashford, personal communication). Depending on weather conditions, it is possible for the larvae to lie in diapause for more than a year (Chris Spencer, personal communication).

## 2.3 References

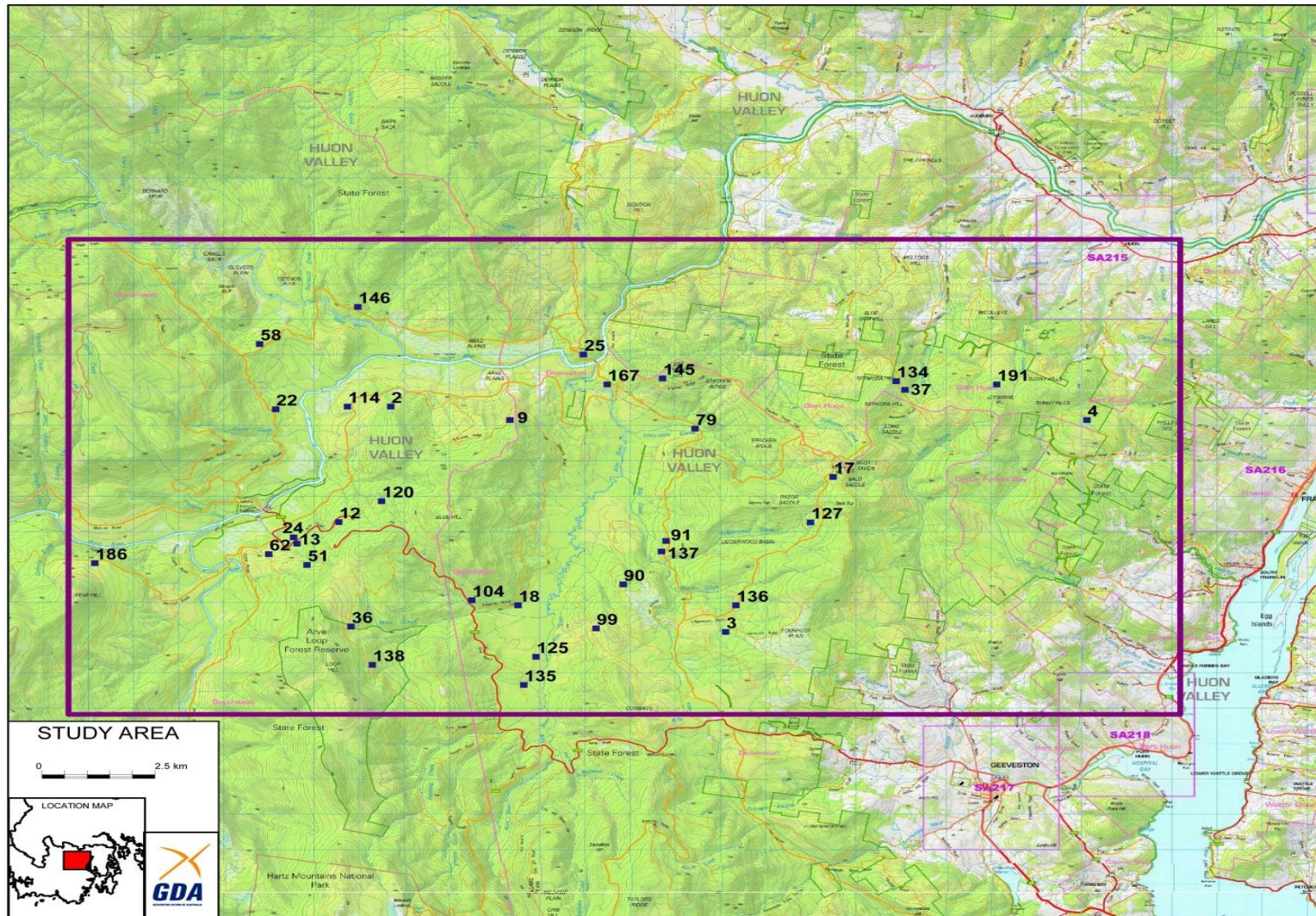
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## APPENDIX 2.1 MAP OF STUDY AREA



A map of the study area (purple border) showing the position of the 35 sites sampled (Table 2.1).

**Research strand a:  
saproxylic beetle  
autecology**

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## **CHAPTER 3 CAN DIFFERENCES IN RELATIVE ABUNDANCE OF TWO SYMPATRIC SPECIES OF *LISSOTES* (COLEOPTERA: LUCANIDAE) BE EXPLAINED BY SPECIES-SPECIFIC SEASONAL PATTERNS OF SEXUAL DEVELOPMENT AND/OR BODY CONDITION?**

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### **3.1 Introduction**

Understanding different life-history strategies between closely related species is important for predicting extinction likelihoods and for conserving species (Davies *et al.* 2004, Brook *et al.* 2008). This typically means acquiring specific knowledge of a species' ecology, and population dynamics. To characterise population dynamics requires knowledge of demography (age and sex structures) and the vital rates of individuals within the population (fecundity, survival, immigration, and emigration). Unfortunately, for many species, particularly invertebrates that are rare or cryptic, or both, this knowledge is lacking and is extremely difficult to acquire. In fact, for many cryptic and rare species, information on demographic rates and processes remains largely unknown.

Saproxylic beetles are an example of an invertebrate group whose population dynamics are poorly understood, owing to the lack of research into their biology and life-history traits (Grove 2006; Davies *et al.* 2008), including sexual development. This is largely due to their saproxylic habits, which oblige them to spend at least part of their life cycle in rotting wood. In this habitat they are often difficult to locate as extracting them requires cutting open logs, which can be dangerous and labour intensive. Even those saproxylic beetles considered widespread can be difficult to find because they rarely appear in large numbers and because they require logs with specific characteristics for their dietary or habitat requirements, attributes that can make their presence sporadic across the landscape.

For species such as saproxylic beetles for which sample sizes are likely to be small, data acquisition must start with collecting data on basic life-history traits such as body weight, and sexual development over seasonal cycles (i.e. traits that can be readily documented in relatively small collections of cohorts or



individuals). Fortunately, these basic traits can offer valuable insights into the population ecology of these species. Measures of physiological characteristics such as the quantity of internal body fat (an indicator of health and condition), the developmental stage of the reproductive organs and ovarian development (in relation to potential fecundity) are important for elucidating the mechanisms of population persistence (Perrin 1991). Moreover, variation in these characteristics can reveal physiological responses to environmental change, affecting population dynamics. For example, if sexual development of a saproxylic beetle is seasonally triggered via accumulated day-degrees then it may respond to, or be moderated by, longer-term changes in climatic variables, a process that could alter annual rhythms in breeding, egg laying and growth; life cycle responses to climate change which have been seen in other beetles. For instance, Butterfield (1996) examined life-history strategies that may enable some species of Carabidae to adapt to climate change, and a study on egg production in two dung beetles found that in one species egg production was less affected by seasonal changes (Ridsdill-Smith 1986). More recent research into how climate change affects the life cycle of beetles is focused around pest species such as bark beetles (Jönsson *et al.* 2007; Bentz *et al.* 2010; Mitton and Ferrenberg 2012) but research into life-history strategies of other saproxylic beetles and climate change is limited. Alternatively there may be a set of hypothetical circumstances with respect to some species' reproductive strategies, which might make one species a superior competitor in a changing climate. For example, the mountain pine beetle is not limited by available hosts but restricted in its range by climatic conditions unfavourable for brooding and future temperature increase is likely to increase its range (Carroll *et al.* 2003).

Body condition is often measured in species in terms of their energetic state, where a species in good condition is assumed to have a greater amount of energy reserves, which it allocates to survival, dispersal and reproductive success. Fitness parameters relating to reproduction have been found to correlate with body condition in many beetles (e.g. carabids: Sota 1985, ladybirds: Dmitriew *et al.* 2009, scarabs: Plaistow *et al.* 2005 and weevils: Bierdermann *et al.* 2011). Elements of body condition such as the quantum of fat reserves can determine whether or not a beetle can survive dormancy (Dijk 1994) or reproduce successfully (Verdú *et al.* 2010) and hence the quantity of fat reserves is a proxy

for health and condition. For example, larvae of the yellow-spotted longicorn beetle, *Psacotha hilaris*, do not enter diapause unless they attain a critical threshold biomass, suggesting the animals' condition is otherwise too poor to survive diapause (Munyiri *et al.* 2004).

In the majority of arthropods, key life-history traits, such as sexual development, respond plastically to seasonality and body condition, which in turn affect population dynamics (reviewed in Higgins and Rankin 1996). In saproxylic beetles, this response may be triggered by a reduction in the distribution and abundance of dead wood, which results in a decrease in food and habitat availability for breeding and egg-laying. Once in a log, food supply is not limiting, however, locating logs becomes more challenging as the number of logs decreases. This places pressure on individuals' food reserves and results in a trade-off between allocating energy to movement versus reproduction. Data on how sexual development changes in response to body condition and season may thus help to understand how the study species have adapted their life-history strategies to living in dead wood.

Recent work on the conservation of saproxylic beetles has dealt mainly with various attributes of their ecology linked to the quantity and quality of dead wood (Yee *et al.* 2001; Wardlaw *et al.* 2009; Sverdrup-Thygeson *et al.* 2010; Sweeney *et al.* 2010; Jackson *et al.* 2012). More extensive research into the life-history traits of this focal group, such as developmental duration, sex ratio, body size and fecundity has the potential to illuminate numerous aspects of ecology (Gerling *et al.* 1986) relevant to their conservation. It may be possible for such information to reveal how beetle populations respond to environmental stress, climatic changes, and habitat modifications (Cheesman 2000; Holland *et al.* 2005; Rink and Sinsch 2011). For instance, a study by Davies *et al.* (2000) found that a morphological difference in body size suggests that larger species of forest beetles subject to landscape fragmentation were more likely to decline than smaller species, and also that taxonomically related species do not necessarily respond the same way to fragmentation. Other basic life-history information can be crucial for assessing the efficacy of current management strategies for saproxylic beetles (Grove 2006). For example, Jonsson (2003) examined life-history traits and colonising ability of two related saproxylic beetles in Swedish forests. *Oplocephala haemorrhoidalis* had poorer dispersal capabilities than its relative *Bolitophagus reticulatus*.

*Bolitiophagus reticulatus* has better-developed flight muscles that allow for short but numerous flights, but less investment in production of eggs. This may put *B. reticulatus* at a greater risk of extinction since low fecundity has been linked to extinction in other saproxylic beetles (Holland *et al.* 2005), but alternatively it may prove to be better adapted to managed forest in which logs are more sparsely distributed.

In this study, the relationship between the condition of the sexual organs, body condition (using body weight and fat-bodies as a proxy for body condition), and season is examined in *Lissotes menalcas* and *L. cancroides*. Information from these previously unstudied species is used to make inferences about their relative abundance and likelihood of extinction in order to assess their conservation status. It is widely accepted that abundance and distribution are interrelated (Brown 1984) but the reasons for differences in the abundance of closely-related, ecologically similar, species are often obscure (Gaston and Blackburn 2000). Current knowledge about the ecological differences between sympatric populations of *L. cancroides* and *L. menalcas* is limited: *L. cancroides* is more widespread and apparently more abundant than *L. menalcas*, which is a threatened beetle (presently classified as ‘Rare’: *Tasmanian Threatened Species Protection Act 1995*) with a patchy distribution across its range.

Many saproxylic beetles possess life-history traits that are thought to lead to low intrinsic rates of population increase (for example, poor dispersal capabilities and small clutch size), but the range of variation in these traits suggests that some species are more vulnerable to local extinction in managed forest landscapes than others (Holland *et al.* 2005). Undertaking preliminary studies of sexual development in Lucanidae may help in understanding why this family of (mostly) saproxylic beetles make up a large proportion of the threatened saproxylic fauna worldwide (e.g. Lachet *et al.* 2012).

*Lissotes cancroides* is more readily encountered in the study-area than its ‘Rare’ relative *L. menalcas* (Section 2.2.1, Chapter 2). In this chapter, I test the hypothesis that inferred differences in relative abundance of two sympatric species, *Lissotes menalcas* and *L. cancroides* can at least partly be explained by species-level differences in seasonal patterns of sexual development and/or body condition (body condition being at least partly dependent on sexual development

stage). To test this hypothesis I developed a simple score-based assessment of the reproductive features and body condition for each sex, and applied this assessment to samples of individuals of both species from multiple sites within the study-area. Evidence of inter-species seasonal variation in these scores was then statistically tested for and the findings discussed in the context of conservation management.

## 3.2 Methods

### 3.2.1 Sampling sites and sampling schedule

Beetles were sampled at monthly intervals from January 2007 to January 2008 at 35 sites in south eastern Tasmania (Appendix 2.1, Chapter 2). See Chapter 2 for a description and map of the study area, and also for a review of the current knowledge regarding the autecology of *L. cancroides* and *L. menalcas*.

Every month an attempt was made to collect at least four males and four females of each study species, though this was not always possible due to time and natural variation in the sampled logs (i.e. some of the logs sampled had few or no individuals). For instance, as *L. menalcas* is distributed sparingly across the study area it was difficult to locate sufficient adults, especially females. *Lissotes menalcas* and *L. cancroides* were sampled directly from the log (whilst gathering the coarse woody debris data analysed in Chapter 5 and 6). The beetles were taken back to the laboratory and stored at -30°C until processing. They were then thawed, weighed and dissected to identify their sexual development over the sampling year.

### 3.2.2 Measuring fat-body quantity and body weight

To investigate body condition and its potential effect on the process of sexual development, I measured fat-bodies and body weight in all individuals.

Individuals were weighed (in milligrams), using a microbalance and the quantity of fat within the body was scored according to the scale of Hardy (1981):

- Score 0 – No fat-body present
- Score 1 – Few strands of fat-body present
- Score 2 – Numerous strands of fat-body present but all abdominal organs clearly visible
- Score 3 – Fat-body appears to fill all interstitial spaces in the abdomen

Weight and fat-body were tested to see whether they were correlated and if so, whether either could be used as a proxy for body condition (validated in Schulte-Hostedde *et al.* 2005).

### 3.2.3 Determining reproductive status

To assess the reproductive schedule of each species, I dissected and qualitatively measured the organs associated with sexual development of all sampled beetles. This information provided an insight into the beetles' reproductive stage at a certain time of the year, for the sampled population. The following scoring system was used to collect qualitative data on reproductive stage.

#### *Scoring reproductive stages in males*

The condition of the accessory glands was scored on the following scale:

- Score 1 – Thin white (sexually immature adults)
- Score 2 – Expanded cream (In frozen specimens - preliminary to forming the spermatophore, which is black and positioned at the junction where the vesicula seminalis diverges from the aedeagus and into the testes)
- Score 3 – Engorged brown (formed spermatophore present)
- Score 4 – Brown and shrunken (spermatophore voided)

The condition of the testes was scored on the following scale:

- Score 1 – Small, rudimentary testes (sexually immature adults)
- Score 2 – Developing an incipient testicular form (transition period)
- Score 3 – Fully developed, large testes (sexually mature adults)

#### *Scoring reproductive stages in females*

The development of the ovaries was scored on the following basis:

- Score 1 – Oocytes not distinguishable, ovariole undifferentiated (sexually immature adult)
- Score 2 – Oocytes ripening and white in colour (transition period)
- Score 3 – Oocytes ripe and ready to be shed from the ovarioles (sexually mature adults)

The condition of the spermatheca in *L. cancroides* and *L. menalcas* was scored on the basis of colour. The progression from white (Score 1), through grey (Score 2) to black (Score 3) is thought to indicate deterioration of the spermatheca and was used as a qualitative measure for the duration of stages in the reproductive cycle. The size progression and quality of the spermatheca was used to determine when the beetle became reproductively receptive (in spring/summer for both species but

also autumn for *L. cancroides*). In addition to the above scoring method, spermatophores were noted if present in the spermatheca and counts were made of obvious eggs (unfertilised and fertilised) as well as discrete oocytes.

### 3.2.4 Data analyses

Chi-square contingency tests were used to assess the significance of season and body condition (using fat-bodies and body weight as a proxy for this) on sexual development. This kind of analysis was deemed appropriate because it is able to test for departures of proportional, ordinal or nominal data from a null hypothesis of no difference among seasons. Seasons were defined as one of the four divisions of the year for temperate zones: summer (December to February); autumn (March to May); winter (June to August); and spring (September to November).

Contingency tests of seasonal variability were performed for the following variables: accessory gland condition, fat-body quantity, presence of mid-gut food, ovarian development, spermatheca condition, spermatophore presence and accessory gland condition.

Seasonal variability in weight and egg number was examined using one-way ANOVA. Two-way ANOVA was used to test for significant seasonal variation between the two study-species in several life-history traits: egg number, body weight, testes condition and accessory gland condition as the measured variable and season as the nominal variable. Post-hoc tests (Tukey-Kramer HSD test) were used to further examine significant results and identify those seasons in which these key traits differed between the two species.

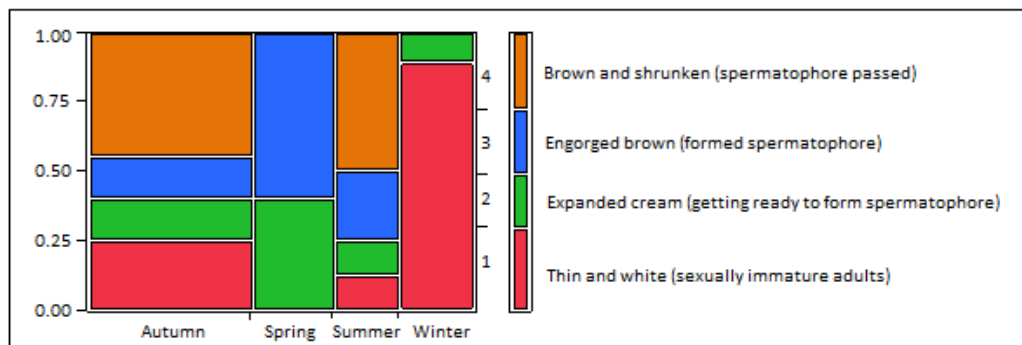
Student's *t*-tests were performed using MS Excel 2007 to compare body weight differences between species, and between different sexes in the same species.

#### *Interpreting the mosaic plots from the chi-squared contingency analysis*

Mosaic plot outputs from the chi-squared contingency analysis were used to illustrate seasonal patterns of reproduction. The mosaic plot in Figure 3.1 is a graphical representation of the two-way frequency table or contingency table. Hartigan and Kleiner (1981) established mosaic plots but they were later refined by Friendly (1994). A mosaic plot is divided into rectangles, so that the area of each rectangle is proportional to the proportions of the Y variable (in the Figure

3.1 example, accessory gland development scores) in each level of the X variable (seasons).

In Figure 3.1 the proportions on the x-axis represent the number of observations for each level of the X variable, which is season. The proportions on the y-axis at right represent the overall proportions of the accessory gland categories: (1) thin white accessory glands (sexually immature adults), (2) expanded cream (getting ready to form the spermatophore), (3) engorged brown (formed spermatophore present); and, (4) brown and shrunken (spermatophore voided) for the combined levels (autumn, spring summer and winter). The scale of the y-axis at left shows the response probability, with the whole axis being a probability of one (representing the total sample). Therefore by consulting the mosaic plot in Figure 3.1 it is inferred that thin and white accessory gland (sexually immature adults) are most prevalent in *L. cancroides* during winter.



**Figure 3.1 Top:** An example of a mosaic plot produced by the  $\chi^2$  contingency analysis of *L. cancroides* accessory gland development and season. The proportion of accessory gland score is expressed as a percentage. For example, in winter 90% of the males had thin and white accessory glands (Score 1). Bars in the key vary with score contribution i.e. an accessory gland score of 2 (represented by the green colour) was least prevalent in the plot.

### 3.3 Results

#### 3.3.1 Body weight is different between species and sex

Table 3.1 shows some descriptive statistics for the body weight of *L. menalcas* and *L. cancroides*. Average body weight of female *L. menalcas* and *L. cancroides* was significantly smaller than that of males ( $t$ -test,  $p < 0.001$ ). *Lissotes menalcas* males and females were significantly larger than *L. cancroides* ( $t$ -test,  $p > 0.001$ ).

**Table 3.1 Body weight descriptive statistics and comparison of weight between sexes and species ( $t$ -test) for *L. menalcas* and *L. cancroides*. \*\*\*,  $p < 0.001$ .**

Species	Sex	Count	Mean weight (g)	Min weight (g)	Max weight (g)	Species difference t-test
<i>Lissotes menalcas</i>	Male	35	0.363	0.117	0.626	***
	Female	32	0.237	0.067	0.394	***
<i>Lissotes cancroides</i>	Male	47	0.118	0.052	0.245	***
	Female	32	0.100	0.040	0.353	***

#### 3.3.2 Quantity of fat-bodies and body weight are positively correlated

There was a strong positive relationship between fat-body quantity and weight, and this applied to males and females of both species (females: *L. menalcas*,  $F_{(1, 30)} = 18.49$ ,  $p = 0.0002$ ; *L. cancroides*,  $F_{(1, 30)} = 10.16$ ,  $p = 0.003$ ; males: *L. menalcas*,  $F_{(1, 33)} = 8.57$ ,  $p = 0.006$  and *L. cancroides*,  $F_{(1, 45)} = 14.79$ ,  $p = 0.0004$  (Figure 3.2). For each sex of both species body weight explained a significant proportion of the variation in fat-body content (*L. cancroides*, males:  $R^2 = 0.24$ ,  $p = 0.0004$ ; females:  $R^2 = 0.25$ ,  $p = 0.003$ ; *L. menalcas*, males:  $R^2 = 0.20$ ,  $p = 0.006$ ; females:  $R^2 = 0.38$ ,  $p = 0.0002$ ).

The results suggested that for this sampled population body weight gives an indication of the amount of fat-bodies; where fat-body quantity increases as body weight increases. Sexual development response to body weight was then tested, with weight being a proxy for body condition (Schulte-Hostedde *et al.* 2005).

#### 3.3.3 Quantity of fat-body and body weight can vary between seasons, but this depends on species and sex.

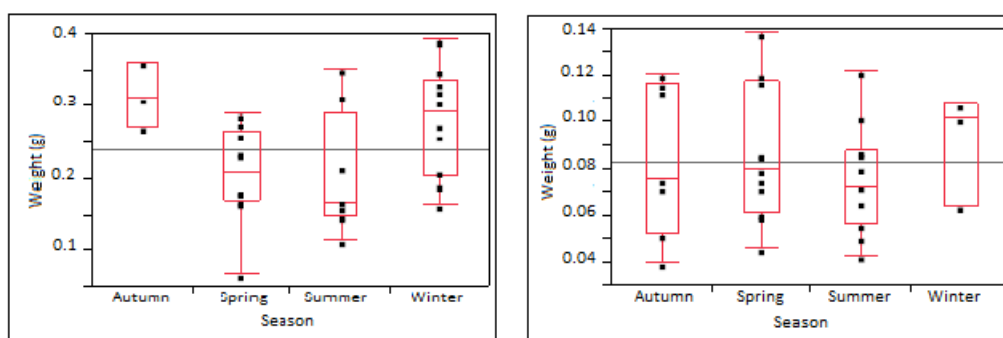
Analyses showed that body weight varies with season for both sexes of *L. menalcas* (males:  $F_{(3, 31)} = 5.46$ ,  $p = 0.0039$ ; females:  $F_{(3, 28)} = 3.42$ ,  $p = 0.03$ ), but



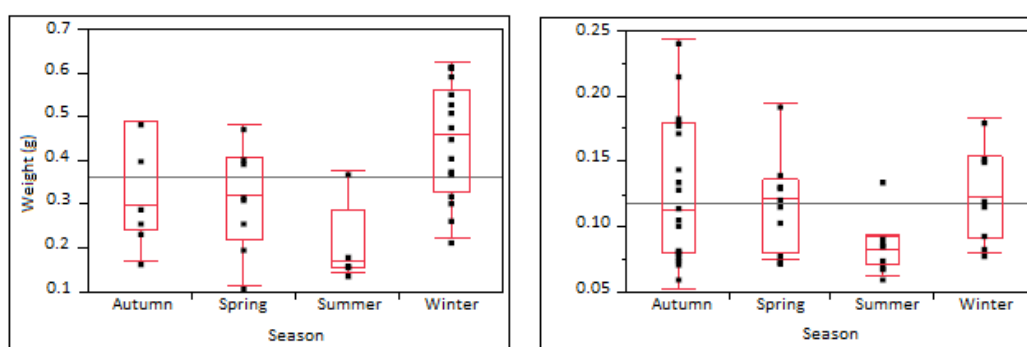
not for either sex of *L. cancroides* (males:  $F_{(3,43)} = 1.73$ ,  $p = 0.17$ ; females,  $F_{(3,28)} = 0.43$ ,  $p = 0.73$ ). Post-hoc analyses indicated that *L. menalcas* weights of males and females differed significantly between summer and winter (Table 3.2), with individuals heaviest in winter and lightest in summer (Figure 3.2 and Figure 3.3).

**Table 3.2 Mean body weight in grams ( $\pm$  se) by season for *L. menalcas* females (left) and males (right). Only the difference between summer and winter is significant (Tukey's HSD).**

Season	n	Mean $\pm$ se	Season	n	Mean $\pm$ se
Autumn	4	0.316 $\pm$ 0.042	Autumn	7	0.340 $\pm$ 0.046
Spring	10	0.207 $\pm$ 0.033	Spring	8	0.316 $\pm$ 0.043
Summer	8	0.204 $\pm$ 0.026	Summer	5	0.211 $\pm$ 0.055
Winter	10	0.282 $\pm$ 0.023	Winter	15	0.449 $\pm$ 0.031

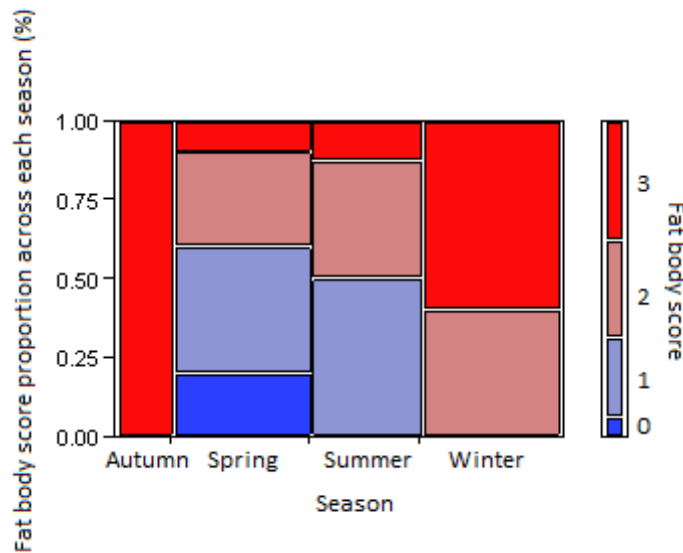


**Figure 3.2 A box and whisker plot of weight (g) per season for females, *Lissotes menalcas* (left) and *Lissotes cancroides* (right).**



**Figure 3.3 A box and whisker plot of weight (g) per season for males, *Lissotes menalcas* (left) and *Lissotes cancroides* (right).**

The fat-body quantity of female *L. menalcas* varied with season ( $\chi^2_{(9, 32)} = 21.26$ ,  $p = 0.025$ ; Table 3.3), with fat-body content greatest in autumn (100% of the females had a fat-body score of 3) and lowest in the spring and summer (20% of the sampled population contained no fat-bodies at these times of year; Figure 3.4). No seasonal variation in fat-body content was observed in male *L. menalcas*, nor in any *L. cancroides*.



**Figure 3.4** Mosaic plot produced from the  $\chi^2$  analysis of fat-body score by season for female *Lissotes menalcas*. The proportion of fat-body score is expressed as a percentage. For example, in autumn 100% of the females have high amounts of fat-bodies (a fat-body score of 3). Bars in the key vary with score contribution i.e. a fat-body score of zero is smallest because this was the least prevalent score in the mosaic plot.

**Table 3.3** Mean fat-body scores ( $\pm$  se) by season for females of *Lissotes menalcas*. Only the difference between summer and winter is significant (Tukey's HSD).

Season	n	Mean $\pm$ se
Autumn	4	2.14 $\pm$ 0.27
Spring	10	2.25 $\pm$ 0.25
Summer	8	1.20 $\pm$ 0.32
Winter	10	2.40 $\pm$ 0.18

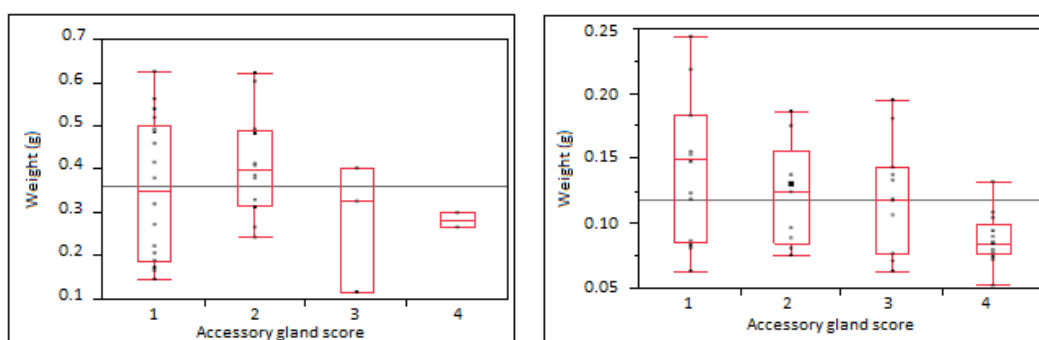
### 3.3.4 Significant relationships between body weight and sexual development are limited to a few measured traits

#### *Body weight and sexual development in males*

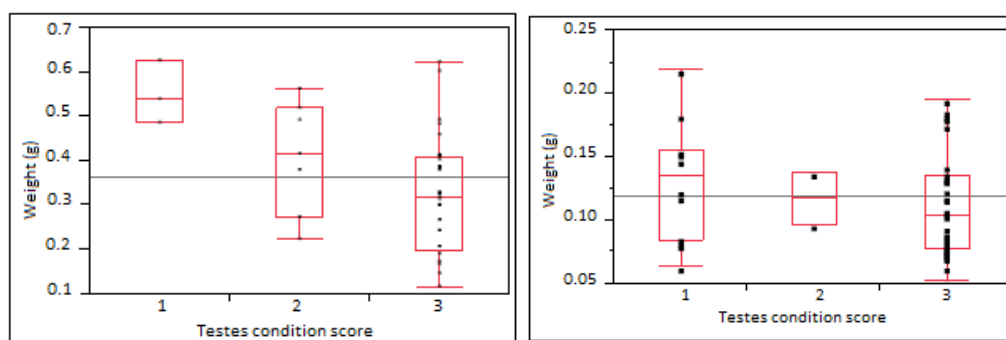
Results revealed a significant negative relationship between body weight and accessory gland condition in male *L. cancroides* ( $F_{(3, 43)} = 4.08$ ,  $p = 0.01$ ) but not body weight and testes condition ( $F_{(2, 44)} = 0.54$ ,  $p = 0.58$ ). Individuals with

undeveloped accessory glands were heavier than those with degrading accessory glands (Figure 3.5, right plot), while the heaviest males exhibited the least developed testes (Figure 3.6).

In contrast, body weight did not vary with accessory gland condition ( $F_{(3, 31)} = 0.99, p = 0.4$ ), but there was a significant negative relationship between body weight and testes condition ( $F_{(2, 32)} = 4.29, p = 0.02$ ) in male *L. menalcas* (Figure 3.6). From the sampled population of male *L. menalcas* it appears that body weight decreases as testes deteriorate (Table 3.4 and Figure 3.6, left plot).



**Figure 3.5** Box and whisker plot of weight by accessory glands in males. Left: *Lissotes menalcas* and right: *Lissotes cancroides*. Accessory gland score 1 – white (sexually immature adults), score 2 – expanded cream (getting ready to form spermatophore), score 3 – engorged brown (formed spermatophore) and score 4 – brown and shrunken.



**Figure 3.6** Box and whisker plot of weight by testes condition. Left: *Lissotes menalcas* ( $p = 0.02$ ), right: *Lissotes cancroides* ( $p = 0.58$ ). Testes condition score 1 – small, rudimentary testes (sexually immature adults), score 2 – developing a more testicular form, score 3 – fully developed, large testes.

**Table 3.4** Mean body weight in grams ( $\pm$ se) by testes condition for *Lissotes menalcas*. All testes condition scores were found to be significant (Tukey's HSD).

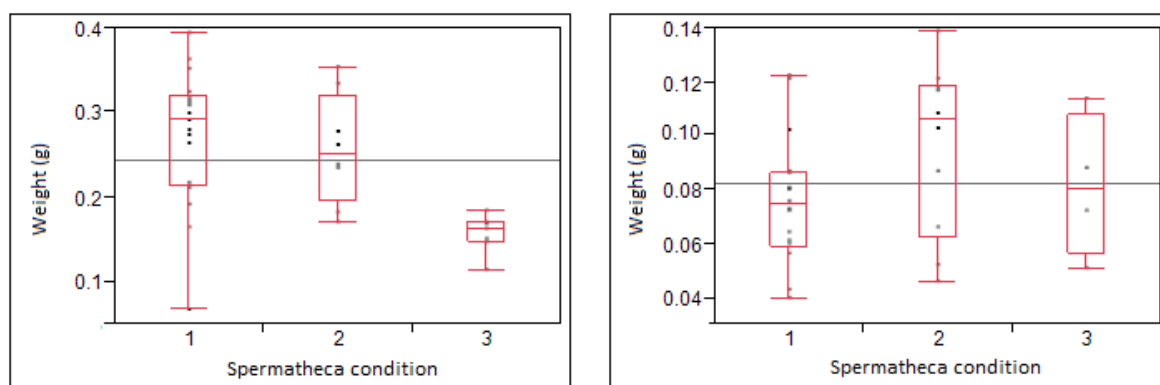
Testes condition score	n	Mean $\pm$ se
1	3	$0.55 \pm 0.07$
2	7	$0.41 \pm 0.05$
3	25	$0.32 \pm 0.02$

### Body weight and sexual development in females

Results revealed a significant negative relationship between body weight and spermatheca condition in female *L. menalcas* ( $F_{(2, 29)} = 7.15, p = 0.003$ ), such that spermatheca condition deteriorated significantly in beetles with low body weight (Table 3.5 and Figure 3.7, right plot). Meanwhile, there was no significant relationship between body weight and the number of eggs produced in either species (*L. menalcas*,  $F_{(1, 30)} = 0.9, p = 0.34$  and *L. cancroides*,  $F_{(1, 30)} = 0.63, p = 0.43$ ).

**Table 3.5 Mean body weight ( $\pm$ se) by spermatheca condition for *Lissotes menalcas*. The difference between spermatheca condition score 1 and 3, and 2 and 3 is significant (Tukey's HSD).**

Spermatheca condition score	n	Mean $\pm$ se
1	17	$0.27 \pm 0.01$
2	8	$0.25 \pm 0.02$
3	7	$0.15 \pm 0.02$



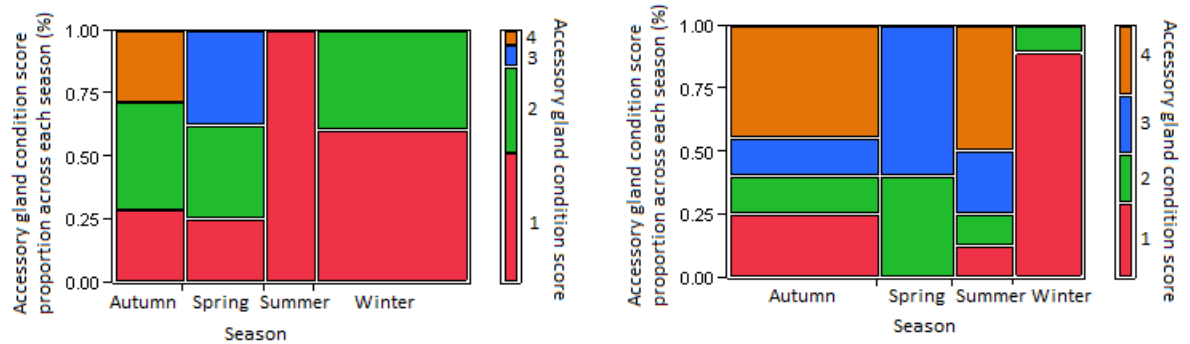
**Figure 3.7** Box and whisker plot of body weight by spermatheca condition in females. Left: *Lissotes menalcas* and right: *Lissotes cancroides*. Spermatheca condition score 1 – white (no deterioration of spermatheca), score 2 – grey (spermatheca start to deteriorate), score 3 – black (spermatheca deteriorated).

### 3.3.5 Seasonal patterns in sexual development depends on species and sex

#### Seasonal patterns in sexual development of males

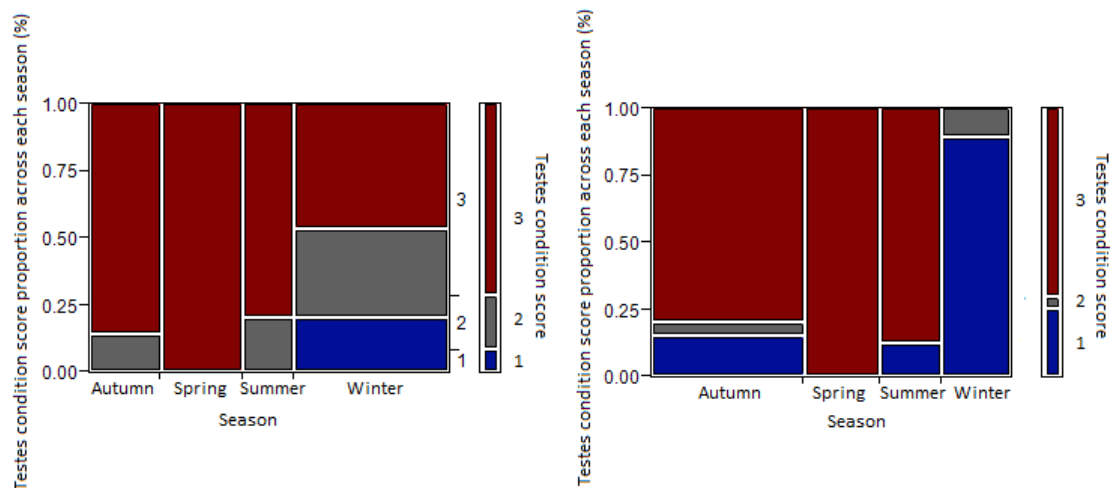
There was a significant relationship between season and accessory gland development for males of both species (*L. menalcas*,  $\chi^2_{(9, 35)} = 24.46, p = 0.003$ ; *L. cancroides*,  $\chi^2_{(9, 47)} = 34.74, p = 0.001$ ). During winter the male accessory glands were thin and white but became cloudy in the latter part of winter suggesting a transition out of the non-reproductive phase by the end of winter (Figure 3.8). The seasonal development of the accessory glands differed between the two study species: in *L. cancroides* the accessory glands were most highly

developed during spring and summer whereas this development was observed in winter and spring for *L. menalcas* (Figure 3.8).



**Figure 3.8** A mosaic plot of accessory gland condition score by season in *Lissotes menalcas* (left) and *Lissotes cancroides* (right). Score 1 – Thin white (sexually immature adults), Score 2 – Expanded cream (preliminary to forming the spermatophore), Score 3 – Engorged brown (formed spermatophore present), Score 4 – Brown and shrunken (spermatophore voided). The proportion of accessory gland score is expressed as a percentage. For example, in summer 100 % of the *L. menalcas* males have an accessory gland score of 1.

Seasonal variation in testes condition, meanwhile, was also observed for males of both species (*L. cancroides* ( $\chi^2_{(6, 47)} = 28.08, p = 0.0001$ ; and marginal significance for *L. menalcas*,  $F_{(6, 35)} = 9.5, p = 0.06$ ), with individuals observed to have fully developed testes in spring and less developed testes in winter (Figure 3.9).

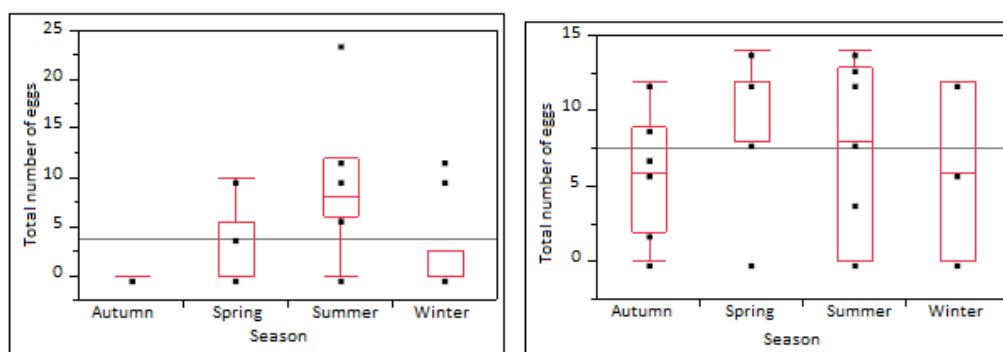


**Figure 3.9** Mosaic plot produced from the  $\chi^2$  analysis of testes condition by season, *Lissotes menalcas* (left) and *Lissotes cancroides* (right). Score 1 – Small, rudimentary testes (sexually immature adults), Score 2 – Developing an incipient testicular form (transition period), Score 3 – Fully developed, large testes (sexually mature adults). The proportion of testes condition score is expressed as a percentage. For example, in autumn, 100 % of sampled population had a testes condition score of 3.

*Seasonal patterns in sexual development of females*

Like their male counterparts, female *L. menalcas* did show seasonality in reproductive condition; specifically, all measured traits showed patterns in seasonality. Sexual development in female *L. cancroides*, however, was less driven by seasonality, with only spermatophore presence varying significantly with season ( $\chi^2_{(3, 32)} = 2.90, p = 0.02$ ).

The number of eggs produced varied with season for female *L. menalcas* ( $F_{(3, 28)} = 4.81, p = 0.008$ ), but not for female *L. cancroides* ( $F_{(3, 28)} = 0.94, p = 0.43$ ) (Figure 3.9). Post-hoc analyses showed that female *L. menalcas* carried the greatest number of eggs in summer (Table 3.6).

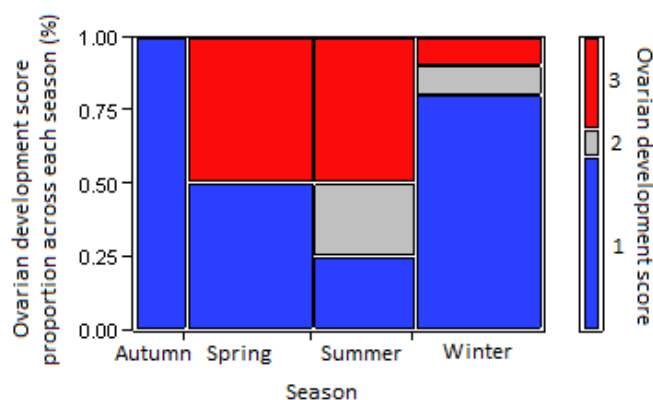


**Figure 3.9** Boxplot of total number of eggs by season for females. Left: *Lissotes menalcas* ( $p = 0.008$ ), right: *Lissotes cancroides* ( $p = 0.43$ ).

**Table 3.6** Mean egg number ( $\pm$ se) by season for *Lissotes menalcas*. The numbers of eggs carried by an individual was significantly different in summer (Tukey's HSD).

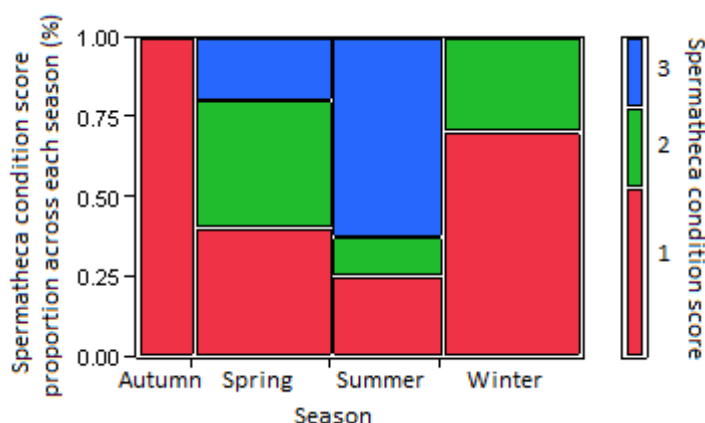
Season	n	Mean $\pm$ se
Autumn	4	0.00 $\pm$ 2.50
Spring	10	2.40 $\pm$ 1.58
Summer	8	9.50 $\pm$ 1.77
Winter	10	2.20 $\pm$ 1.58

Ovarian development also varied seasonally for *L. menalcas* females ( $\chi^2_{(6, 32)} = 11.68, p = 0.02$ ), though underdeveloped ovaries were observed in females throughout all seasons, especially in autumn (Figure 3.10). Follicular differentiation (maturation of ovaries) was observed in spring when oocyte maturation starts to occur and by late spring the ovaries were fully developed. Mature ovaries were also observed in winter (Figure 3.10). Ovarian development did not vary seasonally in female *L. cancroides* ( $\chi^2_{(6, 32)} = 3.55, p = 0.07$ ), with similar numbers of reproductively immature beetles captured in summer as in winter.



**Figure 3.10** Mosaic plot produced from the  $\chi^2$  analysis of ovarian development by season in *Lissotes menalcas*. Score 1 – Oocytes not distinguishable, ovarioles undifferentiated (sexually immature adult), Score 2 – Oocytes ripening and white in colour (transition period), Score 3 – Oocytes ripe and ready to be shed from the ovarioles (sexually mature adults). The proportion of ovarian development score is expressed as a percentage. For example, in autumn, 100 % of the sampled population had an ovarian development score of 1.

Results showed that there was seasonal variation in spermatophore presence for females of both species (*L. menalcas*,  $\chi^2_{(3, 32)} = 9.60$ ,  $p = 0.02$ ; *L. cancroides*,  $\chi^2_{(3, 32)} = 2.90$ ,  $p = 0.02$ ). Spermatophores were present in female *L. menalcas* reproductive tracts predominately during spring and summer and in autumn in female *L. cancroides*. Spermatheca condition varied with season in female *L. menalcas* ( $\chi^2_{(6, 32)} = 15.32$ ,  $p = 0.01$ ), but not female *L. cancroides* ( $\chi^2_{(6, 32)} = 5.44$ ,  $p = 0.48$ ). Only unmated female *L. menalcas* were observed in autumn (spermatheca condition score of 1; pink colour in Figure 3.11), whereas mated females were observed primarily in summer (Figure 3.11). The grey spermatheca condition (Score 2) was observed most frequently in *L. menalcas* during spring.



**Figure 3.11** Mosaic plot produced from the  $\chi^2$  analysis of spermatheca condition score by season in *L. menalcas*. The condition of the spermatheca in *Lissotes cancroides* and *Lissotes menalcas* was scored on the basis of colour. The progression from white (Score 1), through grey (Score 2) to black (Score 3) is thought to indicate deterioration of the spermatheca. The proportion of spermatheca condition score is expressed as a percentage. For example, in autumn, 100 % of the sampled population had a spermatheca condition score of 1.

### 3.4 Discussion

Understanding why populations of sympatric species adopt different strategies requires knowledge of each species' ecology. Unfortunately such knowledge is largely unavailable, specifically for rare or cryptic species such as saproxylic beetles. One approach to making inferences about why two *Lissotes* species differ in abundance is to study the sexual development over seasonal cycles and body condition. The approach in this study makes use of traits that are relatively easy to document. It seems reasonable to use measurable life-history traits as evidence for why sympatric species such as *L. menalcas* and *L. cancroides* differ in abundance and furthermore make inferences about extinction risk and how the beetles may respond differently to future climate change.

Classically, theory suggests that closely related species that use the same resources, and thus directly compete, will either drive each other to extinction (the superior competitor ousting the inferior competitor) or evolve to become specialised in slightly different ways (Harper *et al.* 1961; DeBach 1966; Chunco *et al.* 2012). The evolution of divergent specialisations in competing species can occur when the one species' sexual development responds more plastically to seasonal drivers or to changes in body condition. Species whose reproductive schedules are driven to a greater degree by seasonal variations than by differences in body weight or fat stores, are likely to be disadvantaged when seasonal cues are irregular because being unable to respond to climate variability will result in poor reproductive timing, which may shift the competitive balance with other species and thus, increase extinction risk. When seasonality is more predictable, however, the competitive advantage may shift back to the competing species.

The results of this study have provided some evidence that *L. menalcas* and *L. cancroides* are able to coexist sympatrically in their forest habitat by having differing sexual development across seasons. This is the case for females of both *Lissotes* species, in which sexual development in the 'Rare' *L. menalcas* is more seasonally cued than in the more common *L. cancroides*. In addition, sexual development is largely uninfluenced by body condition, although there is a limited effect of body condition apparent in *L. menalcas*, particularly the females. It is possible that these species are also able to coexist sympatrically because resource allocation into sexual development may differ between the two species.



### 3.4.1 Seasonal patterns in sexual development

Population dynamics are likely to differ between two closely related species when one species' reproductive biology is more seasonally cued (Sota 1987). This is because such species have less opportunity or ability to phenotypically alter the timing or duration of major life cycle events such as diapause and rates of sexual development. For example, in a study of the developmental characteristics in two sympatric species of cricket, one species developed more rapidly under shorter photoperiods while the other showed no response to photoperiod (Tanaka 1986). Such differences in the degree of observed phenotypic plasticity in life-history traits between sympatric species could help to explain why species with extremely similar ecologies can differ greatly in abundance (Harper *et al.* 1961).

In this study, the sexual development of female *L. cancroides* appeared to be less seasonally forced than that of female *L. menalcas*, which affords them a wider temporal window in which to reproduce. Because reproductive success in insects is commonly determined by the female (Rivero *et al.* 2001), the reliance on seasonal cues for reproduction in *L. menalcas* may contribute to its relative scarcity under the climatic conditions present in southern Tasmania today.

### 3.4.2 Body condition changes during the *Lissotes*' sexual development but this change depends on the sex, species and season

Body condition can have important fitness consequences, affecting survival and reproductive rates (Jakob *et al.* 1996), thus influencing population dynamics. In this study, body condition varied with developmental stage of the accessory glands in *L. cancroides* and with developmental stage of the testes and condition of the spermatheca in *L. menalcas*. Since these organs nourish sperm and eggs their condition affects an individuals' probability of reproducing successfully. Previous studies in other insect species have also found relationships between body condition and sexual development. For instance, the testes size of dung beetles appears to be dependent on body condition, measured as somatic weight after controlling for body size (Kotiaho *et al.* 2001). In this study, sexual development in *L. menalcas* responded more strongly to variation in body condition than did sexual development in *L. cancroides*. This suggests that *L. cancroides* needs to invest less energy to reproduce successfully. Although this suggestion remains to be tested experimentally, such a difference in energy

expenditure could result in difference in the population dynamics of these two species.

Energy reserves (in the form of lipid-rich fat-bodies) can determine the reproductive output of insects, depending on their resource allocation strategy (Hahn and Denlinger 2007). In *Lissotes* beetles, as in many other insect species, individuals are likely to accumulate fat reserves during their more actively feeding larval stages, with the reserves then persisting into adult life (Rivero *et al.* 2001; Munyiri *et al.* 2004; Ernsting *et al.* 2008) and the amount of fat reserves a species needs to accumulate may differ depending on its size. If it is the case that larger species that store larger fat reserves have the capacity to survive longer in diapause, then this may explain the larger fat reserves present in *L. menalcas* compared to *L. cancroides*. If we assume that food conversion efficiencies are similar in these sympatric species (both feeding on fungus-infested dead wood of low nutritional quality) then the former species would be expected to develop more slowly. However, it remains unresolved whether in fact *L. menalcas* requires more time to accumulate fat reserves than the smaller *L. cancroides*. The smaller *L. cancroides* cannot physically store as much fat and thus is likely to use up its reserves sooner than its congener. Under this scenario, adult *L. cancroides* would be expected to be in a position to feed and seek mates earlier in the spring than *L. menalcas*. This is the case for some carabid beetles; when access to high quality food is often limited (Ernsting *et al.* 1990; Heessen 1980; Juliano 1986) and their ability to build up fat reserves is affected and compromises their survival in diapause (Djik 1994). In some other beetles, about half the fat reserves are consumed in diapause, leaving half to fuel subsequent dispersal and reproduction (Zhou *et al.* 1995). These allocation ratios in *Lissotes* are not known but the trade-off between dispersal and reproduction could potentially differ between the two species.

As a beetle goes through certain stages of sexual development it allocates body mass (in the form of fat reserves) to nourish sexual organs to become ready to reproduce (Wickman and Karlsson 1989). I found evidence for this in some of the measured traits. For example, beetles showed signs of peak reproductive readiness in sexual organs (accessory glands being most developed, testes and spermatheca condition at their peak and most number of viable eggs present) when they were at their lightest body weight. In contrast, beetles with the greatest body weight were

sexually immature and most commonly found during winter. These individuals are likely to have just eclosed and be full of the fat content laid down in the final larval instar, which is carried through from pupation to adult eclosion. Although it appears that in some cases the beetles are allocating their reserves to sexual development and that weight loss is apparent, the overall amount of weight loss from this process is unknown. In addition, there are other processes that these beetles would need to allocate resources to, such as dispersal. Flightlessness may be one reason that these beetles could invest a large amount of their fat reserves into reproduction, as it is known that flight quickly utilises fat reserves in other saproxylic beetles (Williams and Robertson 2008). But even though the two *Lissotes* species do not fly some energy reserves need to be set aside to crawl in search of logs and mates, and that has to be traded off against reproductive investment and diapause reserves.

### **3.4.3 Can body condition and seasonally forced reproduction explain the difference in abundance of two sympatric species?**

The data accumulated in this study provide an insight into the likely differences in population dynamics of these two sympatric species, and can help to understand their different conservation statuses. *L. menalcas*, listed as a threatened species, appears to have life-history traits that make it more vulnerable to extinction in the face of a changing environment. Results of this study have revealed that (unlike *L. cancroides*) sexual development in *L. menalcas* appears to be attuned to the seasonal cues associated with a predictable climate. In addition, this study has shown that *L. menalcas* has a lower fecundity than *L. cancroides* and a suspected longer life cycle. Long life cycles are a common trait in larger lucanid beetles, for example the European *Lucanus cervus* can live for over three years (Working Group on Iberian Lucanidae 2005) and larger endemic Tasmanian species like *Hoplogonus* spp. have a 2-3 year larval period and can live for up to two years as adult (Karen Richards and Chris Spencer, unpublished data). Characteristics such as low fecundity and long life cycles can predispose species to extinction under changing environmental conditions, and that may make a species more vulnerable to habitat loss and fragmentation (Simberloff 1994).

Habitat loss is not the only environmental pressure likely to increase extinction risk in species which possess life-history traits that negatively impact on species abundance. Climate change is expected to increase over the next few decades and

is predicted to negatively impact on population dynamics and viability of some beetles (Butterfield 1996; Calosi *et al.* 2008; Rink and Sinsch 2011). For example, a selection of life-history traits were studied in the saproxylic beetle, *Lucanus cervus* (Lucanidae), with results suggesting that climate change may increase the vulnerability of local populations by reducing the duration of their activity period (Rink and Sinsch 2011). As female *L. menalcas* appear to rely on seasonal cues to reproduce, they are likely to be particularly susceptible to on-going and future climate change. Alternatively there may be a set of hypothetical circumstances with respect to both species reproductive strategies, which might make *L. menalcas* the superior competitor in a changing climate. For instance, *L. menalcas* may be a stronger competitor under a scenario of highly predictable seasons and low environmental disturbance. Such predictable conditions may have prevailed during earlier epochs when Tasmania was not under the influence of mainland weather systems (e.g. the dominance of El Nino and the aridification of Australia, Cohen *et al.* 2011) as it is today and before Aborigines brought firestick farming to Tasmania (Marsden-Smedley and Kirkpatrick, 2000; Bird *et al.* 2008). Understanding historical and future climate change may indicate how these beetles respond in terms of ‘shifts in space’ and whether we should expect the range of *L. menalcas* (and *L. cancroides*) to be static, contracting or expanding. For southern British butterflies the outlook is positive with modelling demonstrating that numerous species are expanding at their leading-edge range boundaries in response to climate warming (Mair *et al.* 2012). In fact modelling climate change can forecast future distributions for many taxa (Thuiller 2004) including beetles such as carabids (Gillingham *et al.* 2012) and bark beetles (Carroll *et al.* 2003), but it is not always positive. A review by Bellard *et al.* (2012) discusses this ‘shift in space’ as a species response to climate change with a long-term prognosis that suggests for many species their range is expected to contract, giving rise to extinctions.

Life histories are important when considering the impacts of forest fragmentation on populations. For instance, a study by Davies *et al.* (2000) found that larger species of forest beetles subject to landscape fragmentation, were more likely to decline than smaller species, rare species were more likely to decline than abundant ones, and taxonomically related species do not necessarily respond the same way to fragmentation. Field observations suggest that *L. menalcas* is rarer

and more patchily distributed than *L. cancroides*. *Lissotes menalcas* is also larger in terms of size and body weight than *L. cancroides*, and in fact, one of the largest saproxylic beetles in Tasmania. Large body size is known to be correlated with extinction vulnerability in several other beetles (Kotze and O' Hara 2003; Reynolds 2003). This is most likely because larger beetles are less flexible and more specialised than smaller-bodied beetles, traits which are disadvantageous in a changing landscape (Desender and Turin 1989; Gossner and Müller 2011). In the case of the *Lissotes* species the larger body size, patchy distribution and 'Rare' status of *L. menalcas* suggest that it is likely to be less resilient against forest fragmentation than its common, smaller relative *L. cancroides*.

#### **3.4.4 Methodological limitations and interpretative difficulties inherent in the current approach**

A major limitation of this study was that inferences on observed patterns were made on the basis of very small sample sizes, and may not necessarily represent patterns at the population level. Although every effort was made to obtain larger sample sizes, logistical constraints (including difficulties in detecting individuals and the necessity of adhering to the conditions of the collecting permit for the threatened *L. menalcas*) precluded the collection of larger numbers of individuals. Despite this, because the reproductive biology of these particular beetles is largely unknown, any foundation information is important, and as demonstrated above, can provide an intriguing insight into the population dynamics of these two species. Nevertheless, the conclusions presented in this chapter should be interpreted with caution until such time that they can be confirmed in a larger study. Interestingly, a genetic approach may be one way to overcome some of these issues. It may be possible to compare population genetic structures between sympatric species of different abundances and assess the effects of habitat fragmentation through gene flow and genetic variability (Jonsson *et al.* 2003).

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## CHAPTER 4 CAN MOLECULAR TECHNIQUES REVEAL THE FEEDING RELATIONSHIP OF A MYCOPHAGOUS BEETLE? A PRELIMINARY STUDY ON THE TASMANIAN SAPROXYLIC BEETLE *PROSTOMIS ATKINSONI* (COLEOPTER: PROSTOMIDAE)

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### Abstract

The relationship between mycophagous saproxylic beetles and fungi remains largely unknown. To elucidate mycophagy in saproxylic beetles we suggest a comprehensive investigation that requires a multifaceted approach. In this study, we address one aspect of the beetle-fungus relationship by applying molecular techniques to detect fungi in the guts of a Tasmanian saproxylic beetle, *Prostomis atkinsoni*, and the gingerbread rot from decomposing *Eucalyptus* logs, which this species inhabits. Many different types of fungi were detected and there were substantial differences in fungal profiles among the gut and rot samples. Although this is a preliminary study the findings indicate that *P. atkinsoni*, like some other saproxylic beetles, feeds on wood-decay basidiomycetes.

### 4.1 Introduction

Saproxylic fungi and saproxylic insects (those that are dependent on dead wood at some stage in their life cycle) can have an intimate relationship powerful enough to determine their mutual survival (Speight 1989). Previous studies have highlighted the need to manage threats to saproxylic insects and fungi brought about by human use of forests, and this extends to mycophagous saproxylic beetles (Abrego and Salcedo 2013; Müller *et al.* 2007). Further it is widely recognised that successful conservation management requires an underpinning in science (Siitonen 2001; Grove 2002; Davies *et al.* 2008). Hence, as part of a research agenda developed to elucidate the relationships between insects and dead wood (Grove 2006), one of the identified requirements was to develop a fuller understanding of beetle-fungus interactions. In this paper, we report on our attempts to explore these interactions through the application of molecular techniques to detect fungi sampled from a rotten-wood type, ‘gingerbread rot’ (GBR) (Grove *et al.* 2011) and from a saproxylic beetle associated with it, *Prostomis atkinsoni*.

Many saproxylic beetles feed on or in decomposing wood, and it seems highly likely that many derive their nourishment from consuming the fungi that occur there (Hammond and Lawrence 1989; Saint-Germain *et al.* 2007; Tanahashi *et al.* 2009). Wood is composed largely of cellulose, hemicelluloses and lignin. Under normal circumstances these macromolecules are difficult to digest, making it challenging for an animal to obtain any nutritive value from wood (Geib *et al.* 2009; Tanahashi *et al.* 2010). Wood-decay fungi render the nutritional content of wood more accessible, since the fungi secrete digestive enzymes, breaking down these macromolecules into smaller fragments and eventually into their component sugars, and hence facilitating their uptake (Rayner and Boddy 1988).

Additionally, the mycelia, spores and sporocarps of wood-decay fungi represent a potential food-source for saproxylic beetles (Tanahashi *et al.* 2010). Mycophagy can be species-specific. For example, some saproxylic beetles feed only within particular species of polypore fungi, i.e. those that display obvious external fruiting bodies on dead wood (Jonsell and Norlander 2002; Epps and Arnold 2010). Consequently the local complement of fungal species has the capacity to determine local beetle species diversity and composition (Epps and Arnold 2010). Fungal mycelia can also determine future fungal and beetle succession (Persson *et al.* 2011) by changing the nature of the woody substrate. Examples are found among many bark-beetle species of the weevil subfamilies Scolytinae and Platypodinae which are associated with pathogenic and wood-decay fungi in the wood of living trees (Massoumi Alamouti *et al.* 2009);

Surprisingly, the question ‘do the fungi found in particular rotten-wood types provide nutrition for saproxylic beetles, and do beetles feed selectively on them?’ seems to remain unaddressed. There are no known studies in which wood-decay fungi have been found to determine saproxylic beetle succession or presence in decomposing wood.

With the exception of bark beetles, studies on mycophagy in saproxylic beetles have instead generally involved broad surveys that correlated the occurrence of saproxylic beetles and rotten-wood types (Araya 1993; Yee 2005; Wardlaw *et al.* 2009), or observations and surveys of beetles feeding on or reared from external sporocarps. In Sweden over 20 insect species were found to occur in the polypore species *Fomitopsis pinicola* and *Fomes fomentarius*; some of these insects are

red-listed and are restricted to sites in less managed forests (Jonsell and Norlander 2002). In a New Hampshire forest, Chandler (1991) collected over 50 species of fungivorous beetles and found a positive relationship between species abundance and forest age. This type of fungus–beetle relationship is relatively easy to establish because the beetles can be found feeding directly on the fruiting bodies (Martin 1978; Chandler 1991; Jonsell *et al.* 2003), but the beetle–fungus relationship inside dead wood is less readily elucidated (Saint-Germain *et al.* 2007). For instance, Araya (1993) found that a species of Japanese lucanid, *Ceruchus lignarius* was a brown-rot specialist. Araya then performed chemical analyses on the brown rot to identify the decay type and stage of dead wood in which the beetle was found, but did not go to the next stage of isolating or characterising any fungi from the brown rot.

It is a particular challenge to go beyond correlation and to directly establish the existence of mycophagy in saproxylic beetles. Earlier methods in beetles involved microscopy and the staining of gut contents (Ludwig and Hill 1975). More recently, the advent of sophisticated molecular techniques has provided the opportunity to more firmly establish the existence of mycophagy. However, the focus of most molecular research in this area has instead been on examining symbiotic relationships between beetles and yeast or other microbes (Suh *et al.* 2003, 2004), ingested plant material (Wallinger *et al.* 2013) or bacteria (Broderick *et al.* 2004).

To fully investigate how mycophagous saproxylic beetles living within rotten wood obtain their nutrition would require a multifaceted approach, as follows:

- (a) test for the presence of the species' own wood-digesting enzymes or for gut-dwelling symbionts. The presence of either (or both) would indicate xylophagy rather than mycophagy; whereas if neither were present, then this would suggest that any fungi detected in the gut could well have been deliberately consumed as food.
- (b) attempt to isolate fungi from across the range of rotten-wood types potentially available as food, and from the guts of the beetles. If successful, this would allow the fungal assemblages to be correlated,

enabling some tentative inferences regarding mycophagy to be drawn and further hypotheses to be raised.

- (c) conduct laboratory- and field-based food preference studies that investigate the beetles' fungal (and other) food preferences, to explore whether any mycophagy was an obligate or a facultative trait.

Additionally, to elucidate mycophagy and feeding preferences in saproxylic beetles requires an experimental design that ideally focuses on a single species that:

- occurs exclusively in one rotten-wood type in the wood of trees in one genus only;
- is readily detectable and collected;
- is ecologically well understood;
- has known conservation management issues.

Very many saproxylic beetle species live in the wet-eucalypt forests of southern Tasmania (Yee 2005; Grove and Forster 2011), but few meet the above selection criteria. Thus for the present, preliminary study we chose a species (*Prostomis atkinsoni*) that, as a result of related ecological studies on saproxylic beetles (Yaxley, unpublished) had already been determined as meeting all four of these criteria. In particular, its close, almost exclusive association with 'gingerbread rot' (GBR) already strongly indicated that the beetle was at least partly mycophagous rather than xylophagous. Hence we followed approach (b), exploring the mycoflora of the beetles' guts and of GBR.

In pursuing this approach, our primary objective was to test whether current molecular techniques are robust enough to successfully detect fungi from the guts of *P. atkinsoni* and from the GBR in which it lives, with the rationale that if they work for our study-system, then the techniques could be applied more widely. As a second objective, we sought to identify the fungi to a level that would allow us to make meaningful inferences about the fungal microcosm in the GBR and guts of *P. atkinsoni* and mycophagy in this species, and hence to build on the

knowledge-base that could be used to inform management and direct further research efforts.

## 4.2 Materials and Methods

### Sample collection

Beetles and larvae were collected from *Eucalyptus regnans* logs at two locations and from *E. obliqua* logs at a further two locations. Location details are provided in Table 1 and sample details in Table 2. Each beetle, along with a sample of the surrounding rotten-wood type, was placed in a 5 ml vial; 20 samples were collected in this manner. Samples were returned to the laboratory, where the beetles were killed and their gut contents removed and placed into individual 1.5 ml microcentrifuge tubes, while 1 g of the associated rotten wood was placed in a separate tube.

### 4.2.1 Fungal detection

For this initial investigation into the presence of fungi in the guts of *Prostomis atkinsoni*, a DNA technique that did not involve fungal isolation was used. Survival of fungal propagules after ingestion by beetles is uncertain, whereas detection of DNA from dietary components is more reliable (Eitzinger *et al.* 2013). Sequencing the ribosomal DNA internal transcribed spacer region (rDNA ITS) is now a well-established method for fungal identification (Seifert 2009). Fungal-specific primers can be used to selectively amplify fungal DNA from environmental sources (Gardes & Bruns 1993). Fungi from which the DNA is derived can be identified by matching the DNA sequence to one from a known species (Glen *et al.* 2009). Where a close specific match cannot be found, identification may be possible to genus, family or higher level. Whatever the level of identification, the presence of the same fungal DNA in different samples can be detected (Glen *et al.* 2002) with a degree of confidence that is lacking when culture morphology is compared (Hopkins 2007).

### DNA extraction

DNA was extracted from all samples using a PowerSoil DNA extraction kit (MoBio, Carlsbad, USA). Rot samples were first ground in a ceramic mortar and pestle. Beetle guts were ground in a plastic microcentrifuge tube with a motorised plastic pellet grinder (Kimble-Chase, Vineland NJ). A small amount, c. 100 µL, of



buffer from the Powerbead tube in the Powersoil kit was added to facilitate grinding. Ground samples were then added to the Powerbead tube and the manufacturer's standard procedure followed.

#### *Polymerase Chain Reaction (PCR)*

PCR reactions contained Mangotag colourless reaction buffer (Bioline, London), 2 mM MgCl<sub>2</sub>, 0.2 mg/mL bovine serum albumen (Fisher Biotec, Subiaco, Australia), 0.2 mM dNTPs (Bioline, London), 0.25 mM primers ITS1-F (Gardes & Bruns, 1993b) and ITS4 (White *et al.*, 1990) and 1.1 U Mangotag DNA polymerase (Bioline, London) with 5 µL DNA template in a final volume of 25 µL. The thermocycler program consisted of: 2 min. at 95 °C, 35 cycles of (30 s at 95 °C, 30 s at 55 °C, 30 s at 72 °C), followed by 7 min. at 72 °C in a PTC 100 (MJ Research Inc.) or a PCR System 2720 (Applied Biosystems) thermocycler. PCR products were electrophoresed on a 1.5% agarose gel at 10 V/cm for 30 min., stained in 0.1 µg/ml EtBr for 15 min. and visualised on a Vilber-Lourmat (Marne-la-Vallée, France) transilluminator.

#### *Cloning of PCR products*

Amplified DNA was purified using an Ultraclean PCR Clean-up kit (MoBio, Carlsbad, USA), precipitated according to the manufacturer's instructions and resuspended in 13 µL TE buffer (10mM Tris-HCl, pH 8; 1mM di-sodium EDTA). A 3µl aliquot was electrophoresed as above to check concentration. Purified, concentrated PCR products were cloned using a TA Cloning Kit (Promega Corp., Madison, WI, USA) following the manufacturer's instructions. For each sample cloned, 16 white or pale blue colonies were subcultured and a rapid DNA extract prepared by picking a colony with a sterile pipette tip and adding it to 200 µL of TE buffer in one well of a 96-well PCR plate. The wells were capped, the plate vortexed to disrupt bacterial cells, and centrifuged to pellet cell debris. The supernatant was used as template in PCR.

#### *Screening of colonies by PCR-RFLP*

A 5 µL aliquot was used as template in a 50 µL PCR using primers ITS1-F/ITS4 as described above. PCR product (5 µL) was digested in separate reactions with restriction enzymes Alu I and Taq I (Glen *et al.* 2002) then electrophoresed on a 3% Resolution Plus agarose (Progen Industries Ltd, Darra, Qld) gel at 4 V/cm for

5 h. Two or three colonies from each PCR-RFLP group were selected for DNA sequencing. The remaining 35 µL of undigested PCR product was sent to Macrogen Inc, Seoul, N. Korea, for sequencing.

#### *Analysis of DNA sequences*

Chromatograms were viewed and edited in the Seqman module of the Lasergene package (DNASTar, Madison, USA). Public DNA databases were searched for matching sequences using Blastn (Altschul *et al.* 1990). Sequences were aligned using ClustalW (Li 2003) and those with >98% similarity were grouped into operational taxonomic units (OTUs). Where possible, OTUs were identified to species or genus by sequence similarity to known, morphologically identified isolates or herbarium specimens and categorised into functional groupings.

#### Assigning fungal functional groups

Species that occurred frequently and that could be identified to the level of family or higher were placed into one of five fungal functional groups according to their ecological role. The functional groupings were:

- (i) Wood rotting basidiomycetes (species of *Botryobasidium*, *Phlebia* and *Serpula*, and an OTU with affinities to Hymenochaetales)
- (ii) Trichocomaceae – species of *Aspergillus* and *Penicillium* are ubiquitous fungi commonly associated with decaying plant material
- (iii) Leaf spot fungi – species of *Colletotrichum* and *Teratosphaeria* are best known as causal agents of leaf spot diseases (Cannon *et al.*, 2012, Hunter *et al.*, 2011).
- (iv) Endophytes – Species of *Cladophialophora*, *Oidiodendron* and *Phialocephala* have been isolated from woody tissues and characterised as dark septate endophytes (Vohník & Albrechtová, 2011; Addy *et al.* 2005).
- (v) *Candida* spp. – Yeasts of this genus have been widely reported as gut inhabitants of arthropods and may be endosymbionts (Grunwald *et al.* 2010).

## 4.3 Results

### 4.3.1 Fungi can be identified from the guts of *P. atkinsoni* and the surrounding GBR

PCR, cloning and sequencing enabled the detection of 72 fungal OTUs in the guts of *P. atkinsoni* and in the surrounding GBR (Supplementary Table 1). Eight of the OTUs were identified to species or aff. species level, 14 were identified to the level of genus and another three were placed into families (Table 3). The majority of OTUs (47 of the 72) could be identified only to the level of kingdom (i.e. Fungi) or phylum (Ascomycota or Basidiomycota). Criteria for identification of each OTU are provided (Supplementary Table 1), along with the accession numbers of representative sequences.

### 4.3.2 Distribution of Operational Taxonomic Units among the gingerbread rot and guts of *P. atkinsoni*

Fungal species diversity differed among samples. The majority of fungal OTUs were detected in a single sample each, with only 20 OTUs occurring in more than one sample (Table 4). From the gut samples, 41 fungal OTUs were detected, and 38 from the surrounding rot. Of the 72 fungal OTUs detected only seven were found in both *Prostomis* guts and the surrounding wood-rot: Ascomycete spp. 14 and 15, Basidiomycete spp. 2, 14, 15 and 16, and *Teratosphaeria parva*.

The lack of overlap between species found in guts and those found in rots may be explained by the rarity of most OTUs, with 52 recorded from only one sample each. Only five of the OTUs were found in more than four samples; Basidiomycete sp. 2 was found in seven gut samples and six rot samples, *Coniophora aff. olivacea*, *Aspergillus* sp. 1 and *Pleurotus australis* were detected in nine, six and five gut samples, respectively and Basidiomycete sp. 15 was found in two gut and three rot samples, (Table 4).

#### 4.3.2.1 Functional diversity of fungi found in *P. atkinsoni* guts and GBR

Several functional groups can be recognised from the fungi found in the rot and gut samples (Table 5). *Pleurotus*, *Coniophora*, *Serpula*, *Botryobasidium* and the Hymenochaetales are known wood rotters (Wardlaw 2003), and it is likely that

Basidiomycete sp. 2 is also, as the closest DNA sequences in the INSDs (International Nucleotide Sequence databases) were polypore fungi.

*Aspergillus* and *Penicillium* are closely related genera of fungi that in this study were found predominantly in beetle guts. These genera are ubiquitous and species commonly ferment starchy substrates and may frequently be associated with decaying plant material (Bennett 2010). Two of the OTUs were found in 4 or 6 samples, the remainder were infrequent.

The genera *Colletotrichum* and *Teratosphaeria* are not closely related, but include species of known leaf pathogens (Cannon *et al.* 2012, Hunter *et al.* 2011). Four species of *Colletotrichum* and two of *Teratosphaeria* are therefore grouped together based on their life mode rather than taxonomic affinities.

Another functional group contains 7 OTUs that include species of *Oidiodendron*, *Phialocephala*, *Cladophialophora* and related species. These are common endophytes and saprobes in woody plants and some species may be weakly pathogenic to plants. Species of *Oidiodendron* are commonly isolated from decaying wood, bark and humus (Hambleton *et al.* 1998). Species of *Phialocephala* are also commonly isolated from plants (Addy *et al.* 2005). The natural habitat of *Cladophialophora* spp. is rotting plant material, though some species cause disease in humans and animals (Badali *et al.* 2008). These OTUs were found mainly in beetle guts, though several were in rot samples only or in both guts and rots.

Three species of *Candida* and other ascomycetes with affinities to *Candida* spp. (e.g. Ascomycete sp 10) were found in six beetle gut samples. *Candida* sp. 1 occurred in three samples, the rest in one or two each.

#### 4.4 Discussion

Fungi can be detected in the gut of *P. atkinsoni* and surrounding gingerbread rot. Molecular methods were successful in detecting fungi directly from beetle gut contents and their rotten wood habitat. Previous analyses of beetle gut contents to determine the presence of fungi have relied either on fungal isolation or staining and microscopy to discern fungal material. Microscopy provides poor taxonomic discrimination of the fungi involved (Hugo *et al.* 2003). Isolation methods

facilitate identification of the fungi isolated but are more selective than PCR (Suh *et al.*, 2006, Ji *et al.* 2009).

Over 40 fungal OTUs were detected from 20 beetle guts, with up to seven OTUs detected in a single larval gut. Previous molecular analyses of invertebrate gut contents have mainly targeted invertebrate prey (Sheppard & Harwood 2005), though some have examined ingested plant material (Wallerger *et al.* 2013) or bacteria (Broderick *et al.* 2004). Wallinger *et al.* (2013) showed that plant DNA can be detected in wireworm gut contents for at least 72 h after ingestion, but that detection success rate was less than 100% even immediately after ingestion.

A similar number of OTUs (39) was detected in the rotten-wood samples. Tasmanian eucalypt forests have a high fungal diversity, including wood-rotters as well as ectomycorrhizal fungi that may also inhabit rotting wood (Ratkowski and Gates 2009; Gates *et al.* 2009; Tedersoo *et al.* 2009; Gates *et al.* 2011). Gates *et al.* (2011) identified 410 species of macrofungi associated with CWD in *E. obliqua* forest in Tasmania, of which 195 had been formally described. Fungi isolated from rot pockets in the wood of living *E. obliqua* trees included 91 OTUs, of which a large proportion could not be identified even with the aid of DNA sequencing (Hopkins *et al.* 2011). This contrasts with some northern temperate regions, where mycological studies have a longer history and where ecosystems tend to be simpler because of the more severe effects of recent glacial cycles. For example, a study of fungal diversity in aspen dead wood in Canada found 31 fungal OTUs (Kebli *et al.* 2012). In Norway a study of fungi inhabiting 543 spruce logs from five forests across southern Norway yielded 109 OTUs (Rajala *et al.*, 2012). These studies all included larger sample sizes and the whole spectrum of rot types whereas our investigation was based on much smaller sample numbers and the single rot type that was associated with *P. atkinsoni*.

Many fungi were detected in the gut contents of *P. atkinsoni* and from the surrounding gingerbread rot; however, there was very little correspondence between the two. The fungal species detected in both sample types were diverse in their ecological functions and some may represent gut colonisers with potential roles in assisting digestion or preventing colonisation by pathogens. Others are more likely to have been consumed but whether this was intentional or inadvertent

remains uncertain, and the benefits to *P. atkinsoni* provided by dietary fungi will require further work to clarify. Feeding choice experiments, larval development on diets restricted to a particular fungus and the feeding of antibiotics to free beetle guts of endosymbionts have all been used in other beetle species (Tanahashi *et al.* 2009).

It is difficult to determine whether the presence of saproxylic beetles is related to specific fungi within dead wood and it is even more difficult to establish their presence based on nutritional needs. In terms of functional quality, dead wood is a poor food source, even when fungi make the nutrients more accessible. However, beetles may be associated with specific fungi because the fungus is of higher nutritional value; this value may differ depending on a beetle's life cycle stage (Adams and Six 2007). Because fungi are such an important component of the diet they can affect insect development, and fungi that provide poor nutrition can affect size and reproduction (Adams and Six 2007). Nutritional provisioning by fungi is important for successful development and reproduction in beetles, and not all fungi are likely to be equivalent in their ability to provide nutrients (Adams and Six 2007; Abrahamsson *et al.* 2008).

#### **4.4.1 Fungal functional groups and the potential role they play in the guts of *P. atkinsoni* and surrounding gingerbread rot**

We managed to identify many of the operational taxonomic units to the level of family or genus and in some cases species level and assigned these better known species to five functional groups. We assigned fungal functional groups for two reasons; firstly to help understand more about the fungal microcosm in the GBR and guts of *P. atkinsoni* and secondly, to investigate whether grouping the fungi could offer any insight into how *P. atkinsoni* obtains nutrition from GBR.

##### **Wood-decay basidiomycetes**

The most frequently detected OTUs in beetle guts were basidiomycete wood-decay species, in which we include the unidentified Basidiomycete sp. 2. Only seven of the 72 OTUs were identified as wood-decay basidiomycetes and only four of these were detected in the GBR. It is possible that more of the 22 unidentified basidiomycetes are also wood-decay species. They may be rare species or have been in low abundance at the time of sampling.

While an association between the beetles and wood-decay fungi is clear, it would be necessary to conduct food preference experiments to determine whether they feed on these fungi or not. Whether the wood-decay basidiomycetes are deliberately chosen by the beetles or merely consumed by chance as the beetles graze the rotten wood is beyond the scope of this study, but previous research indicates wood-decay fungi contribute to saproxylic beetle nutrition. For example, Tanahashi *et al.* 2009 fed mycelia of several wood rotting fungi (including *Pleurotus* sp.) to the Japanese *Dorcus rectus* (Lucanidae) to demonstrate that this species is fungivorous and larval body mass increases on a diet of wood-decay fungi. The wood-decay fungus Basidiomycete sp. 2 may be a food source for *P. atkinsoni*, it was found in seven gut samples and six rot samples, but only one of these was a corresponding pair, i.e. the beetle was taken from that particular rot sample. *Pleurotus australis* and *Coniophora aff. olivacea* were detected in five and four beetle guts, respectively, but not in any of the GBR samples. This could indicate that sampling of the GBR was inadequate to detect the full suite of fungi within the rot sample as DNA was extracted from only a small sample of the rot whereas the entire insect gut was processed. Little work has been done to determine the sample size needed for molecular analysis of fungal communities in complex, heterogeneous substrates such as soil or rotting wood. Techniques utilising next generation sequencing rather than cloning will facilitate the analysis of larger sample sizes and numbers which will allow a more robust analysis of the influence of factors such as tree species and life stage.

Alternative hypotheses for the disparity between species found in beetle guts and those found in the surrounding rot may include (i) grazing on the surrounding rot types, (ii) preferential consumption of these species or (iii) a long residence time in the gut for certain fungal propagules with high resistance to digestion. These are discussed below.

The beetles may be foraging in parts of the CWD that were not sampled. Field observations indicate that *P. atkinsoni* is found predominantly in GBR, this rotten wood type may provide physical conditions that are necessary for its survival. For example, the flattened appearance of GBR may be created by *P. atkinsoni*

physically packing down the rot, an action that may proffer survival by creating essential habitat requirements rather than dietary ones.

Preferential consumption of certain desirable fungal species may also contribute to the discrepancy between fungi found in beetle guts and those found in the surrounding rot. Species such as *Pleurotus australis* and *Coniophora aff. olivacea* may be particularly attractive to *Prostomis atkinsoni*. One way to confirm this would be to conduct feeding preference experiments *in vitro*, a technique that has been applied to study mycophagy in other saproxylic beetles (Tanahashi *et al.* 2009). Field experiments have also been used to demonstrate feeding preferences. Beetles that visited sporocarps of *Fomitopsis pinicola* and *Fomes fomentarius* in Norway were mainly saproxylic species and most had a preference for one or the other of the two fungal species (Hågvar 1999). Species of the obligatory mycophagous Oxyporinae can be divided into five groups according to their feeding preferences (Hanley and Goodrich 1995). One group consumes a broad range of fungal species without any preference for particular species; another consumes a broad range but prefers a smaller subset of species; the third group consumes a narrow range without any preferences; the fourth has particular preferences within a narrow range and the last group consists of beetle species that feed on a single fungal species.

The third potential explanation for fungi being detected in beetle guts and not in the surrounding rot is related to the residence period of DNA or fungal material in the insect gut. The longer the residence time, the greater the chance of the DNA being detected after the insect has moved away from the site at which the fungus was ingested. Residence time of fungal DNA in the guts of *P. atkinsoni* is unknown though it is likely that DNA within resistant propagules has a longer residence time than DNA in mycelia. Survival and longevity of fungal spores in insect guts have been investigated for a few species of invertebrates including a species of *Drosophila* (Diptera: Drosophilidae) (Coluccio *et al.* 2008) and *Ceratophysella denisana* (Collembola) (Nakamori and Suzuki 2010). The survival of a spore during passage through the gut appears to be dependent on several factors, including the strength of its cell wall and what stresses it is put under prior to entering the gut (e.g. grinding action of mandibles). *Coniophora*, *Phlebia* and *Serpula* species have resupinate sporocarps that commonly occur in dark,



confined spaces such as the underside of logs and could conceivably be found inside logs, in which case basidiospores could be consumed by the larvae.

Basidiospores of some *Coniophora* species and *Serpula lacrymans* have thick cell walls with up to five distinct layers so may be resistant to digestion (Keller 1973). In addition, *Coniophora* species form chlamydospores, which have very thick cell walls (Bigelow 1998). Species of *Pleurotus* have also been observed to form chlamydospores in culture and in colonised wood blocks (Marryat 1908).

#### Leaf pathogenic fungi

The presence of *Colletotrichum* and *Teratosphaeria* species in the GBR and in the beetle guts was unexpected. The four OTUs assigned to *Colletotrichum* were not identified to species level so little is known about their ecological roles. *T. molleriana* is a well-known leaf pathogen of eucalypts (Hunter *et al.*, 2011) and *T. parva* is known from the leaves of eucalypts and other plant species, though is considered less likely to be phytopathogenic (Crous 1998). Field observations show that *P. atkinsoni* inhabits disused termite galleries and foraging ants or termites may have returned leaf material to their nests inside CWD.

#### Trichocomaceae

*Aspergillus* and *Penicillium* are large and ubiquitous genera, each consisting of several hundred species. These have previously been isolated from the digestive tracts of grasshoppers (Ademolu and Idowu 2011), bees (Kacaniova *et al.* 2009), coffee berry borers (Perez *et al.* 2003; Gama *et al.* 2006), a wood borer (Delalibera *et al.* 2005), termites (Mahalingam *et al.* 2007), triatomines (de Moraes *et al.* 2004) and earthworms (Alonso *et al.* 1999; Sudha 2010; Chhotaray 2011), including food-free earthworm guts (Byzov *et al.* 2009). Several *Aspergillus* and *Penicillium* species are considered to be normal inhabitants of the intestinal flora of many arthropods as well as larger animals including humans (Bennett 2010). There is no compelling evidence of an obligate symbiotic relationship and several studies indicate that arthropod hosts are able to digest cellulose and lignin even if fed antibiotics to eliminate gut microflora (Tanahashi *et al.* 2009). Genta *et al.* (2006) determined that gut symbiont fungi of *Tenebrio molitor* (Coleoptera: Tenebrionidae) are not essential for digestion but may assist in digestion of refractory compounds and play a role in detoxification of secondary plant compounds. Earthworms are possibly the most studied

invertebrates in terms of gut microflora and studies indicate that *Aspergillus* and *Penicillium* spp. resist digestion and are avoided as a food source (Dash *et al.* 1980). However, earth worms are associated most often with soil and not decomposing wood; therefore, the presence of *Aspergillus* and *Penicillium* in the guts of invertebrates associated with wood, such as termites, boring beetles and saproxylic beetles like *P. atkinsoni*, indicates these fungi may play some role in the diets of these invertebrates.

#### Endophytic fungi

Species of *Cladophialophora*, *Oidiodendron* and *Phialophora* are well-known as root endophytes (Bergemann and Garbelotto 2006; Kernaghan and Patriquin 2011). They are often grouped, along with *Cadophora*, *Cylindrocarpon* and others, under the collective term ‘dark septate endophytes’ because of the characteristic appearance of their hyphae and are found in a broad range of woody and non-woody plants. Despite their near ubiquity, much remains to be learnt about their roles in these plants (Peterson *et al.* 2008). Members of this group may be associated with ericoid and ecto-mycorrhizae (Mandyam and Jumpponen 2005). *Phialophora* species have also been reported as foliar endophytes in conifers with a potential role in controlling insect herbivory (Sumarah *et al.* 2009). The perception that these fungi colonise only the roots of their hosts may be a misapprehension encouraged by the large number of studies based on below-ground plant parts. Relatively few studies examine endophytes in woody stems and branches. Menkis *et al.* (2004), by contrast, isolated DSE fungi from tree roots, live stems and both coarse and fine woody debris of *Pinus*, *Picea* and *Betula* forests in Sweden. It is likely that these fungi are normal inhabitants of wood and may be consumed either deliberately or inadvertently by *P. atkinsoni*.

#### Ascomycete yeasts

*Candida* species have been isolated from or detected in the digestive tracts of many insects including nitulid beetles (Suh *et al.* 2006), sand flies (Akhoundi *et al.* 2012), cockroaches (Zheltikova *et al.* 2011), grasshoppers (Ademolu & Idowu, 2011), the wood borers *Apronia germari* (Hui *et al.* 2012), *Odontotaenius disjunctus* and an unidentified log-dwelling tenebrionid (Houseknecht *et al.* 2011), Neuroptera (Nguyen *et al.* 2007) and in mycetomes in the gut of wood-inhabiting cerambycid beetles (Grunwald *et al.* 2009). Suh *et al.*

(2008) isolated *Candida* species from the guts of several Coleoptera, including species in the Elateridae, Chrysomelidae and Scarabaeidae. *Candida* species have also been found in association with rotten wood (Wang *et al.* 2010) but in this study the *Candida* and related species were detected only in beetle guts and not in the GBR. *Candida* species may assist in the fermentation of xylose (Cadete *et al.* 2012).

#### Unidentified fungi

The vast majority of fungi detected, 52 of the 72OTUs, were unable to be identified below the level of phylum. This is consistent with studies of fungal diversity in eucalyptus ecosystems, which are characterised by high biodiversity and a relative paucity of information (Glen *et al.* 2002). Some of the unidentified sequences may represent fungi that are known to science but for which rDNA ITS sequences are not yet available, and others may represent unknown and undescribed fungi. As fungal bar-coding initiatives provide more comprehensive and reliable sequence databases, the percentage of unidentified OTUs is expected to decrease, though unknown fungi are likely to continue being detected for the foreseeable future.

## 4.5 Conclusions

*Prostomis atkinsoni* is an obligate log-dweller that inhabits decaying *Eucalyptus* logs. In this study, we applied molecular techniques to isolate fungi from the gut contents of *P. atkinsoni* and the recently categorised rotten-wood type ‘gingerbread rot’ that this species inhabits more or less exclusively. Many different types of fungi were detected and there was great diversity in fungal profiles among the gut and rot samples. In addition, there was very little correspondence among the fungi found in the rotten wood and the gut. Several explanations were given as to why *Coniophora aff. olivacea*, a well-known wood-decay fungus, was consistently found in the guts but not in the rot; further work is needed to explain this unexpected result. The fungal species detected in both sample types were diverse in their ecological functions. We could not prove that the fungi detected in the guts were a part of *P. atkinsoni*’s diet, nor could we establish that *P. atkinsoni* is selecting particular fungi from gingerbread rot; further food preference experiments and field studies are needed to address these

gaps in knowledge, but this study indicates it is likely that *P. atkinsoni*, like some other saproxylic beetles (Tanahashi *et al.* 2009), feeds on wood-decay basidiomycetes.

The molecular technique used in this study provided an initial insight into potential mycophagy in *P. atkinsoni*; however, we are constrained in what we can definitively conclude. A broader application of this type of molecular approach will give a better understanding of mycophagy in saproxylic beetles and hence the implications of how we manage their dead-wood resource.

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**Table 1 Location of study sites including aspect and broad forest type defined by the FC 2001 system.**

Site	General area	Broad forest type (treatment)	GDA eastings	GDA northings	Aspect
4	New Road Sp 2 Geeveston	Un-aged regrowth (eucalypt) with mature eucalypt	496125	5231150	South
13	Arve Rd, Geeveston, near Spur 1	Mature eucalypt forest with un-heighted regrowth	478625	5227650	South
24	Arve Rd, Geeveston	Un-aged regrowth (eucalypt) with mature eucalypt	478550	5227825	North
51	Arve Spur 2 Geeveston	Mature eucalypt forest without regrowth	478850	5227050	South

**Table 2 The 20 *Prostomis atkinsoni* samples used in the analysis. Site details are provided in Table 1.**

Life stage	Host tree species	Sample code	Collection date	Site
adult	<i>E. regnans</i>	1023	10/09/2008	4
adult	<i>E. regnans</i>	8962	10/09/2008	4
adult	<i>E. regnans</i>	2565	10/09/2008	4
larva	<i>E. regnans</i>	6496	10/09/2008	4
larva	<i>E. regnans</i>	7077	10/09/2008	4
larva	<i>E. regnans</i>	7556	10/09/2008	4
larva	<i>E. regnans</i>	530	10/09/2008	4
larva	<i>E. regnans</i>	9733	10/09/2008	4
adult	<i>E. regnans</i>	3888	23/07/2008	51
adult	<i>E. regnans</i>	4746	23/07/2008	51
larva	<i>E. regnans</i>	9432	23/07/2008	51
adult	<i>E. obliqua</i>	8887	20/08/2008	13
larva	<i>E. obliqua</i>	5032	20/08/2008	13
larva	<i>E. obliqua</i>	1800	20/08/2008	13
larva	<i>E. obliqua</i>	2446	20/08/2008	13
adult	<i>E. obliqua</i>	6524	25/08/2008	24
larva	<i>E. obliqua</i>	3233	25/08/2008	24
larva	<i>E. obliqua</i>	4409	25/08/2008	24
larva	<i>E. obliqua</i>	9919	25/08/2008	24
larva	<i>E. obliqua</i>	9201	25/08/2008	24

**Table 3 Fungal OTUs, detected from *P. atkinsoni* guts (G) and surrounding wood rot (R), that were identified to the level of species, genus, family or order.**

OTU	Class, Family	Detected in guts (G) and/or rot (R)
Basidiomycota		
<i>Pleurotus australis</i>	Agaricales, Pleurotaceae	G
<i>Coniophora aff. olivacea</i>	Boletales, Coniophoraceae	G
<i>Serpula aff. himantoides</i>	Boletales, Serpulaceae	G
<i>Botryobasidium</i> sp.	Cantharellales, Botryobasidiaceae	R
Hymenochaetales sp. 1	Hymenochaetales, <i>incertae sedis</i>	R
<i>Phlebia</i> sp. 1	Polyporales, Meruliaceae	R
Ascomycota		
<i>Teratosphaeria parva</i>	Capnodiales, Teratosphaeriaceae	R
<i>Teratosphaeria molleriana</i>	Capnodiales, Teratosphaeriaceae	GR
<i>Cladophialophora aff. australiensis</i>	Chaetothyriales, Herpotrichelliaceae	G
<i>Aspergillus aff. conicus</i>	Eurotiales, Trichocomaceae	G
<i>Penicillium</i> sp. 1	Eurotiales, Trichocomaceae	G
<i>Penicillium</i> sp. 2	Eurotiales, Trichocomaceae	G
<i>Penicillium aff. diversum</i>	Eurotiales, Trichocomaceae	G
Trichocomaceae sp. 1	Eurotiales, Trichocomaceae	R
Trichocomaceae sp. 2	Eurotiales, Trichocomaceae	R
<i>Colletotrichum</i> sp. 1	Glomerellales, Glomerellaceae	G
<i>Colletotrichum</i> sp. 2	Glomerellales, Glomerellaceae	G
<i>Colletotrichum</i> sp. 3	Glomerellales, Glomerellaceae	G
<i>Colletotrichum</i> sp. 4	Glomerellales, Glomerellaceae	G
<i>Oidiodendron</i> sp. 1	Leotiomycetes <i>incertae sedis</i> , Myxotrichaceae	G
<i>Oidiodendron</i> sp. 2	Leotiomycetes <i>incertae sedis</i> , Myxotrichaceae	R
<i>Phialocephala</i> sp. 1	Ophiostomatales, Ophiostomataceae	G
<i>Candida</i> sp. 1	Saccharomycetales	G
<i>Candida</i> sp. 2	Saccharomycetales	G
<i>Candida</i> sp. 3	Saccharomycetales	G

**Table 4 Fungal OTUs in individual gut and rot samples, in order of abundance (G indicates the OTU was detected in beetle or larval guts, R indicates the OTU was found in the rotten wood surrounding the insect). Singletons (OTUs detected in only one gut or rot sample) indicate the number of OTUs unique to a particular sample.**

Tree Species	<i>Eucalyptus regnans</i>										<i>Eucalyptus obliqua</i>									
Site	4	4	51	51	4	4	4	4	51	4	24	13	24	13	13	24	24	13	24	24
Life Stage <sup>1</sup>	A	A	A	A	A	L	L	L	L	L	A	A	L	L	L	L	L	L	L	L
OTU\Sample code	1023	2565	3888	4746	8962	6496	7077	7556	9432	9733	6524	8887	530	1800	2446	3233	4409	5032	9201	9919
Basidiomycota sp. 2				GR		G		G		G	GR	R	R	R	G	R	G			
<i>Coniophora olivacea</i>					G	G	G	G			G			G	G		G			G
<i>Aspergillus</i> sp. 1		G			G			G								G			G	
<i>Pleurotus australis</i>		G				G								G		G	G			
Basidiomycota sp. 15				G				R						R	GR					
<i>Penicillium aff. diversum</i>						G		G								G	G			
<i>Teratosphaeria molleriana</i>				G			G					R					G			
Basidiomycota sp. 14							G	GR							R					
Ascomycota sp. 3	R				R		R													
Ascomycota sp. 11										G					G	G				
Ascomycota sp. 17									R					R	R					
<i>Colletotrichum</i> sp. 1		G	G							G										
Ascomycota sp. 15				G			R			G										
Ascomycota sp. 10					G		G													
Ascomycota sp. 14									G			R								
Ascomycota sp. 16									G							G				
Basidiomycota sp. 1											R	R				R				
Basidiomycota sp. 16					GR															
<i>Candida</i> sp. 1			G						G											
<i>Teratosphaeria parva</i>				R								R								
Singletons (gut) <sup>2</sup>	1	1		1	1	1	2	3	1		3	2			2	3		3		1
Singletons (rot) <sup>2</sup>	1		1		2	1	3	1	3	1		4	1	3	1			3	2	

<sup>1</sup>A = adult, L = larva. <sup>2</sup>Singletons indicates the number of OTUs that were detected in a single gut or rot sample.

Table 5. Fungal functional groups based on fungal OTUs in Table 3

Fungal functional group	Fungal OTUs	Group number
Wood-decay Basidiomycetes	Basidiomycete sp. 2	1
Other wood-decay Basidiomycetes	<i>Pleurotus australis</i> <i>Phlebia</i> sp. 1 <i>Serpula</i> aff. <i>himantioides</i> <i>Botryobasidium</i> sp. <i>Hymenochaeta</i> sp. 1	2
<i>Coniophora</i> (brown rot)	<i>Coniophora</i> aff. <i>olivacea</i>	3
Trichocomaceae	<i>Aspergillus</i> aff. <i>conicus</i> <i>Aspergillus</i> sp. aff. <i>restrictus</i> <i>Penicillium</i> sp. 1 <i>Penicillium</i> sp. 2 <i>Penicillium</i> aff. <i>diversum</i> Trichocomaceae sp 1 Trichocomaceae sp 2	4
Leaf fungi	<i>Colletotrichum</i> sp. 1 <i>Colletotrichum</i> sp. 2 <i>Colletotrichum</i> sp. 3 <i>Colletotrichum</i> sp. 4 <i>Teratosphaeria parva</i> <i>Teratosphaeria molleriana</i>	5
Endophytes	Ascomycete sp. 12 Ascomycete sp. 14 Ascomycete sp. 15 <i>Cladophialophora</i> aff. <i>australiensis</i> <i>Oidiodendron</i> sp.1 <i>Oidiodendron</i> sp.2 <i>Phialocephala</i> sp. 1	6
<i>Candida</i> group	Ascomycete sp. 10 <i>Candida</i> sp. 1 <i>Candida</i> sp. 2 <i>Candida</i> sp. 3	7

**Research strand b:  
saproxylic beetles and  
dead wood**



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## CHAPTER 5 CAN AN EXPLORATORY TECHNIQUE AND A MODELLING APPROACH IDENTIFY THE LOCAL COARSE WOODY DEBRIS (CWD) HABITAT REQUIREMENTS OF SIX SAPROXYLIC BEETLES IN WET-EUCALYPT FORESTS OF SOUTHERN TASMANIA?

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### 5.1 Introduction

Worldwide interest in the conservation of saproxylic beetles has increased in recent years following the discovery that, in some regions, a large proportion of these species are threatened with extinction. For example, in Sweden, 80% of IUCN red-listed forest insects, the majority of which are beetles, (Ehnström *et al.* 1993; Jonsell *et al.* 1998) are dependent on habitat containing coarse woody debris (CWD). Throughout Europe, saproxylic beetles comprise the majority of red-listed beetles because long-term, intensive and inappropriate forest management practices have caused substantial declines in CWD habitat (Juutinen *et al.* 2008). As a result, authorities have now set conservation targets to increase CWD habitat in many parts of Europe. In contrast, intensive forest management is a comparatively new phenomenon in Tasmania and there remains the opportunity to carefully manage CWD habitat to allow saproxylic beetles to persist in landscapes subject to timber harvesting. The effective management of CWD habitat for saproxylic beetles requires a robust understanding of their preferences for particular CWD habitat attributes. In this chapter I attempt to thoroughly characterise the habitat preferences of six saproxylic beetles (*Lissotes menalcas*, *Lissotes cancroides*, *Prostomis atkinsoni*, *Coripera deplanata*, *Dryophthorus* ECZ sp 02 and *Toxeutes arcuatus*) by using predictive habitat models to identify their preferred CWD attributes. The following subsections introduce specific CWD attributes that are thought to enable saproxylic beetle presence in CWD.

#### 5.1.1 Coarse woody debris attributes can determine species occurrence

Comparing patterns of species occurrence and abundance with characteristics of dead wood habitat in forests subject to natural disturbances and varying types of harvesting activities can establish species' habitat preferences and allow the habitat attributes contributing to variation in species diversity to be identified. To date, the majority of studies investigating such patterns have used field-collected data from just a handful of sites (Økland *et al.* 1996; Bishop *et al.* 2009; Brin *et*

*al.* 2009), while few have exploited the wealth of information readily available in forestry databases (Davies *et al.* 2008). In this study, database information was combined with field measurements of dead-wood attributes to provide a more accurate understanding of the habitat requirements of saproxylic beetles and the probability of their occurrence.

#### *Decay stage*

Saproxylic beetles have a complex relationship with rotten wood and the fungi and microorganisms that create it (Chapter 4). In recent years, studies examining ecological processes and the pathways to wood decomposition (decay stages) have identified not only the organisms responsible for decay, but also the communities of organisms associated with them or with the products of their actions (Wardlaw *et al.* 2009; Grove *et al.* 2011). Whilst these studies have shown that the decay stage and type of decaying dead wood (see below) can be classified and modelled throughout time, the influence decay stage has on the occurrence and abundance of saproxylic beetles is largely unknown (Yee 2005). Furthermore, studies conducted in Tasmania have revealed that a five-category decay classification scale can explain a substantial amount of the variation in biomass loss throughout decomposition of CWD, but cannot characterise the complexity of the ecological processes giving rise to this loss (Grove *et al.* 2011).

#### *Rotten-wood types*

Harmon *et al.* (1986) define rotten wood as that which has undergone some degree of decomposition from biotic or abiotic processes, or a combination of both. These processes include the physical and metabolic actions of various organisms such as bacteria, xylophagous arthropods, and basidiomycete and ascomycete fungi. These organisms can change the physical, chemical and biological properties of wood (Rayner and Boddy 1988) and give rise to specific rotten-wood types (Ausmus 1977; Harmon *et al.* 1986). For example, white-rot fungi alters wood cells by removing lignin, cellulose and hemicellulose; a process that leaves the wood bleached and either spongy, stringy or laminated (Kaarik 1974). Brown-rot fungi also break down cellulose and hemicellulose, but not lignin (Cowling 1961).

Very few studies to date have investigated the occurrence of saproxylic beetles in relation to rotten-wood types. Araya (1993) showed that, in general, lucanid beetles in a cool temperate broad-leaved forest of central Japan were not

significantly associated with particular rotten-wood types, though two species were concentrated on brown rot and one species on soft rot. In contrast, a recent study in the wet-eucalypt forests of southern Tasmania demonstrated that there were clear associations between certain assemblages of saproxylic beetles and various rotten-wood types, in *Eucalyptus obliqua* logs (Yee, *et al.* 2004; Yee 2005). The study of Yee (2005) included a far greater number of rotten-wood types than that of Araya (1993), suggesting that the higher the diversity of rotten-wood types in wet-eucalypt forests contributes to important associations between saproxylic beetles and rotten wood.

### **5.1.2 Dead wood is an important structural legacy**

Particular attributes of dead wood are proven to increase the probability of occurrence in some saproxylic beetles (Section 5.1.1) and studies have shown that dead wood post-disturbance is an important structural legacy. Dead wood left after clearfelling operations is thought to play an important role in ecosystem recovery after disturbance (Franklin *et al.* 2000). Dead wood not only contributes to the restoration of biodiversity post-disturbance, but also determines the abundance and spatial arrangement of remnant populations of beetles, factors that are fundamental to the persistence of different species in the production-forest matrix. Hence, characterising the preferred dead-wood microhabitats of beetles can facilitate actions designed to maintain legacy CWD and dead wood input into the substrate, and can thus promote the persistence of beetles in otherwise unfavourable conditions. In forests, the importance of pre-existing structural legacies (i.e. the forest structure that remains after disturbance) like coarse woody debris has been identified for other plants and animals (Franklin *et al.* 2000; Lindenmayer *et al.* 2006). In a checklist of measures for forest biodiversity conservation Lindenmayer *et al.* (2006) state that at the forest-stand level the retention of dead trees and large fallen logs is critical. The structural legacy that remains after logging operations have ceased depends on forest management practices, particularly rotation lengths, which if too short can deplete areas of dead wood. For example, Grove and Stamm (2011) found that when activities such as clearfell, burn and sow occur over more than one rotation they can diminish legacy CWD. Hence, short rotations may produce a living stand that is not old enough to provide sufficient CWD habitat for the persistence of saproxylic species.

### 5.1.3 Hypothesis and aims

In this chapter I attempt to establish if CWD attributes can determine species presence/absence by testing the hypothesis that an exploratory technique and modelling approach can successfully identify local CWD habitat requirements of six saproxylic beetles in wet-eucalypt production forests of Tasmania.

Correspondence analysis explored the preferences of the study species for different types of rotten wood at the finest scale and then statistical models (boosted regression trees and boosted generalised linear models) were developed to identify the CWD and CWD-site attributes (CWD-site attributes that have direct influence on log environment) that best predict species occurrence at the CWD-scale. To test the hypothesis and thus explain the presence/absence of the study species the following aims were established: (1) describe the specific microhabitat (rotten-wood types) requirements of six saproxylic beetles within wet-eucalypt production forest in Tasmania, (2) using the selected modelling techniques define specific CWD habitat requirements of six saproxylic beetles within wet-eucalypt production forest in Tasmania. The associations between the saproxylic beetles and the CWD and CWD-site habitat requirements are then discussed.

The following criteria defined why *Lissotes menalcas*, *Lissotes cancroides*, *Prostomis atkinsoni*, *Coripera deplanata*, *Dryophthorus* ECZ sp 02 and *Toxotes arcuatus* were appropriate candidates for this study:

- they all occur in sufficient numbers to obtain reasonable sample sizes
- they all occur in wet-eucalypt forest
- they all occur in CWD and are thought to be either xylophagous or mycophagous.

Note that Chapter 6 builds on the fine-scale analyses conducted in this study to identify other environmental variables at greater spatial scales by modelling beetle presence at the site- and landscape-scale. In so doing, these chapters constitute an attempt to determine the data required to accurately predict species occurrence at various spatial scales (see Section 1.3.6 for a discussion on the modelling approach), and ultimately, to determine the most informative spatial scale for predicting occurrence of the study species. Using data from different spatial scales

to predict species occurrence has been used elsewhere to successfully model incidence of saproxylic species (Thomaes *et al.* 2008; Bergman *et al.* 2012; Lassauce *et al.* 2012; Musa 2012). Interest in predictive habitat models is increasing because these models are tools that help to understand species habitat requirements, their spatial distributions, and can also provide insights into likely future ecological impacts of environmental change (Guisan and Thullier 2005; Hirzel *et al.* 2006).

## 5.2 Methods

### *Association between rotten-wood types and species presence*

#### 5.2.1 Data collection

Fieldwork was conducted from 9 November 2006 to 15 February 2009. The study area was located in the southern wet-eucalypt forests of Tasmania. These forests lie west of the town of Geeveston (43°04' S, 146° 41" E), which is a 1.5 hour drive from the capital city, Hobart (see Chapter 2 for full details of the study area). Logs were sampled along line intersect transects that were arranged in a cross as this sampling technique has been shown to reflect true volume and mass of CWD in wet-eucalypt forests of Tasmania (Woldendorp *et al.* 2004). Transect lines were 100 m in length and ran either in a north-south or east-west direction (200m of transect line in total). Every log that intercepted the transect line and was  $\geq 5$  cm in diameter and  $\geq 1.5$  m length was sampled. These dimensions were chosen based on the ecology of the study species and because logs of this size could be sampled in the same fashion.

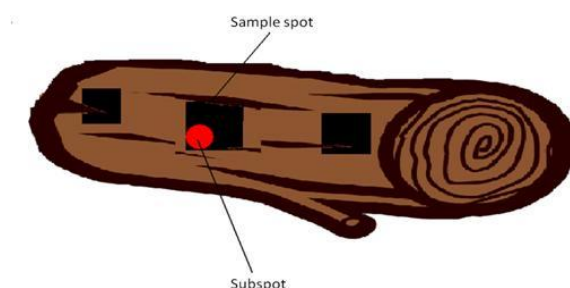
Each log was cut with an axe at either three (logs <20m in length) or four (logs >20m in length) 'sample-spots' along the log (Figure 5.1). Sample-spots were located within a metre of each end of the log and in the middle of the log (one spot in the middle for smaller logs, two for larger logs). The depth and width of sample-spots was largely determined by the degree of decay. A log in the later stages of decay was easier to cut into than one in the early stages of decay, allowing more rotten wood to be sampled.

Every sample-spot on a log was searched thoroughly to locate the six study species (see Table 5.1). When a study species was located and removed from the sample-spot the area it was directly in contact with was referred to as the 'sub-

spot' (Figure 5.1). The rotten wood extracted from each sample-spot and sub-spot was examined by hand and its characteristics noted (see below).

### *CWD predictor variables*

The rotten wood extracted from sample-spots and sub-spots was allocated to one or more rotten-wood types according to the descriptions of Yee (2005) and Stamm (2006) (see Table 5.2 and Appendix 5.1 for detailed descriptions of each rotten-wood type). To avoid confusion with wood-rotting fungi (i.e. brown rot and white rot: Yee 2005; Stamm 2006; Hopkins 2007) certain rotten-wood type names have been changed to 'dark' and 'pale' (Table 5.2). The rotten-wood type 'gingerbread rot' (GBR) was newly identified during this project, and is thought of as a dark rotten-wood type. No rot (NOR), wet cracks (WCR), humus (HUM), humus-soil and charcoal (CHA) are not classed as rotten wood, but were included as they are ecologically significant features of logs. The proportion of the sample-spot area occupied by each rotten-wood type was calculated.



**Figure 5.1 Sampling position in a piece of CWD, showing the relationship of sample-spots and sub-spots.**

**Table 5.1 Study species and their codes.**

<b>Saproxylic beetle species</b>	<b>Species code</b>
<i>Prostomis atkinsoni</i>	Pa
<i>Coripera deplanata</i>	Cd
<i>Lissotes menalcas</i>	Lm
<i>Lissotes cancroides</i>	Lc
<i>Toxeutes arcuatus</i>	Ta
<i>Dryophthorus</i> ECZ sp. 02	Dt

**Table 5.2 A list of types of rotten wood recognised in this study and their abbreviations (Grove *et al.* 2011). \* Not a rotten-wood type but interspersed amongst rotten wood or considered an important feature of the decomposing CWD.**

<b>Rotten-wood types or CWD feature</b>	<b>Code</b>
*Charcoal	CHA
Dark blocky crumbly rot	DBC
Dark blocky fibrous rot	DBF
Dark borer wood	DBW
Discoloured wood	DIW
Dark stringy rot incipient	DSI
Dark stringy rot	DSR
*Frass from <i>T. arcuatus</i>	FRA
Fibrous surface rot	FSR
Gingerbread rot	GBR
*Humus-soil	HSO
*Humus	HUM
Jelly surface rot incipient	JSI
Jelly surface rot	JSR
Brown mudgut rot	MUD
Pale pocket rot	PPR
Pale spongy rot	PSP
Pale stringy rot	PSR
*Wet cracks	WCR
*No rot	NOR

### 5.2.2 Correspondence Analysis (CA) of relationship between microhabitat variables and species presence

Correspondence analysis (CA) was used to visualise the relationship between the presence of saproxylic beetles and particular rotten-wood types because the data were tabulated as counts (Kroonenberg and Greenacre 2005; Greenacre 2007). Correspondence analysis (CA) represents species and samples as occurring in a postulated environmental space, or ordination space (Greenacre 2007). An important assumption of CA is that species have unimodal species response curves. In CA, a species is located at the ordination space where it is most abundant. In this study, species abundance relates to how associated the study species is to a broad or narrow range of rotten-wood types. This method was chosen because it is robust to datasets that contain very low counts; in this case, species occurring at low frequency or in few samples (note however, that *Toxeutes arcuatus* was omitted from the CA analysis because it occurred at very low frequencies; see Greenacre (2011)). Correspondence analysis produces a convenient bi-plot output which displays the association between the rows (beetles) and columns (rotten-wood types) of the dataset on one plot (as spatial convergence on the  $x$ - and  $y$ -axes). Hence, associations between species and rotten-wood types were determined based on the proximity of the rotten-wood type to the study species in the CA plot.

Correspondence analysis was used to visualise associations between the type of rotten wood and (a) the combined counts of larvae and adults of each species; and (b) the counts of the adults of each species in isolation. These analyses were then repeated using the incidence of each species (i.e. presence/absence) as the metric used (which places equal weight on all non-zero observations).

As the study species were found all year round, time (i.e. month or year) was not included in these analyses. Correspondence analyses were computed using R version 2.8.1 (R Development Core Team 2008).

### 5.2.3 The influence of CWD attributes on beetle presence

Every CWD sampled was given a numerical identifier and each sample spot an additional identifier (i.e. L10S1, L10 = CWD number 10 along transect and S1 = sample-spot one on that log). At each sample-spot on every log sampled, the



following variables were recorded: *decay class*, proportion of *rotten-wood type* (%), *burnt* (yes/no), *diameter of log*, *volume sampled* (calculated by length x width and depth of sample-spot), *log length*, *decay class*, *log decay class*, *species present* and *larvae or adult*, *log off ground*, *log cut*, *log burnt*, *tree species* and *close to log end* (see Table 5.3 for full details). In addition, for each log in which the study species were found the following characteristics were also noted: what tree species the CWD was derived from, if the CWD was burnt or not and if the log was on or off the ground (see Table 5.3 for full details). All these environmental covariates were included in predictive habitat models. This first set of modelling the presence/absence of the study species includes not only the CWD variables but local variables at a site; variables that can act at a local or site level have been called CWD-site variables. These CWD-site scale predictor variables can greatly influence the CWD environment (and therefore CWD attributes) so it was important to include at this level and to distinguish them from the CWD variables. The CWD-site variables are (explained in Table 5.4): *age of regen* (age of regenerating forest), *volume of dead wood* (CWD), *diameter sampled cm*, *Rgr*, *Rgen* and *Mat/Rgr* (regenerating forest from silviculture or natural disturbance), *most recent fire*, *broad forest class*, *forest class*, *log decay class* and *dominant eucalypt species*.

**Table 5.3 CWD variables used for predictive habitat modelling (not all variables were chosen by the model ).**

<b>Variable name</b>	<b>Explanation of variable and/or why variable was chosen</b>	<b>Format (units)</b>
Diameter at intersect		Continuous (cm)
Volume of sampled spot on log	Length x width x depth	Continuous (cm <sup>3</sup> )
Proportion of rotten-wood type	Expressed as a percentage. Identifies what rotten-wood type is dominant at the sample-spot	Continuous
Rotten-wood type	One of twenty rotten-wood types characterised (Table 5.4). May elucidate species preferred habitat at the CWD scale	Categorical (20 types)
Log length		Continuous (m)
Decay class (at sample-spot)	See Table 5.6	Ordinal (1-5)
Log decay class	An estimate of the decay class for an entire log	Ordinal (1-5)
Log off ground	Identifies a log was located off the ground	Nominal (Y,N)
Log burnt	Identifies a log was burnt or charred	Nominal (Y,N)
Log cut	Identifies a log that has been cut (not fallen naturally)	Nominal (Y,N)
Species present	Which one of six species is present	Categorical (Pa, Dt, Lc, Lm, Ta, Cd)
Adult or larva	What life stage are the species sampled	Categorical(A,L)
Number of individuals	May determine species presence i.e. a large number of individuals on a specific rotten-wood type may indicate that a species has a preference for this rotten-wood type.	Continuous (count)
Tree species	Tree species the CWD is derived from. Beetles may be associated with CWD from a particular tree species (Table 5.5)	Categorical (14 types)
Close to log end	Identifies the sample-spots which are close to the end of a log. End of log is more exposed to elements, it may display different rotten-wood types than further inside the log and it also provides easy access inside CWD	

**Table 5.4 CWD-site predictor variables used for predictive habitat modelling of the study species. \* see text for further details.**

Variable name	Descriptors	Explanation of variable and why variable was chosen
Age of regenerating forest*	1898 to 1999	Year when forest regeneration began. Affects volumes and heterogeneity of CWD.
Volume sampled	cubic centimetres per hectare	Volume of rotten-wood sampled may be a proxy for presence (how much volume of rotten-wood had to be sampled before a beetle was found)
Volume of dead wood (CWD)*	cubic metres per hectare	Volume of CWD ( $\text{m}^3 \text{ha}^{-1}$ ) may relate to amount of accessible habitat for saproxylic beetle.
Diameter sampled cm	Centimetres	The diameter of the log where it intersects the transect line. Provides the average diameter classes at a site - informally defines proportion of CWD sizes at a site.
Close to log end	true or false	Identifies the sample-spots which are close to the end of a log. End of log is more exposed to elements, it may display different rotten-wood types than further inside the log and it also provides easy access inside CWD.
Rgr, Rgen and Mat/Rgr	Rgr= natural regrowth element of eucalypt stand Rgen=silvicultural regeneration of eucalypt stand Mat=mature eucalypt stand	Identifies the origins of the eucalypt stand and if the tree growth is derived from natural or silvicultural means. Management history may affect forest type and structure. It may also influence CWD volumes and heterogeneity.
Most recent fire	1898-1914, 1934, 1966-67, 1969-74, 1979-83, 1992-99	Year of most recent fire event for each site. These years were grouped according to fire frequency occurrence over time. Fire affects forest type, structure and CWD volume and introduces charcoal to CWD.
Broad forest class	See Table 5.7	Broadly defines stand structural attributes which may identify current and future CWD quantity and quality.
Forest class	A numbered code used by Forestry Tasmania to identify stand structural attributes at the CWD-site (Table 5.7, Chapter 5)	Identifies in detail forest-stand structural attributes which may identify current and future CWD quality and quantity

### *Tree species*

Table 5.5 lists the tree species from which the dead wood was derived.

**Table 5.5 A list of the tree species from which CWD was derived.**

<b>Tree Species</b>
<i>Anodopetalum biglandulosum</i>
<i>Acacia dealbata</i>
<i>Acacia melanoxylon</i>
<i>Atherosperma moschatum</i>
<i>Bedfordia salicina</i>
<i>Cyathodes glauca</i>
<i>Eucryphia lucida</i>
<i>Eucalyptus obliqua</i>
<i>Eucalyptus regnans</i>
<i>Melaleuca squamea</i>
<i>Nothofagus cunninghamii</i>
<i>Nematolepis squamea</i>
<i>Olearia argophylla</i>
<i>Pomaderris apetala</i>

The intention was to allocate each log to one of five decay classes proposed by Meggs (1996) and previously applied in several studies of CWD dynamics in Tasmania (Grove 2000; Yee 2005; Stamm 2006, Grove *et al.* 2009; Grove *et al.* 2011). However, classifying all samples to these five decay classes proved difficult - a problem previously encountered by Gates (2009). Hence, in the current study, nine decay classes were used (based on those proposed by Gates, 2009) to accommodate different wood species and overcome the problems associated with uneven intervals between decay classes (Gates, 2009; Table 5.6).

The variable *tree species* was collected in the field (see Table 5.5 for tree species names), while the remaining predictor variables were obtained from particular forestry maps and databases provided by the GIS division of Forestry Tasmania; such variables include *broad forest class*, *forest class*, *regeneration class*, *most recent fire*, *age of regenerating forest* and *forest type*. Dead-wood volumes were calculated from the line intersect transect by measuring the diameter and length of each log that intersects the transect line and applying the Van Wagner formula (Van Wagner, 1968). The volume estimates were calculated in m<sup>3</sup> ha<sup>-1</sup> for each site.

**Table 5.6 Decay stage classification system for CWD in wet-eucalypt forest (adapted from Meggs 1996)**

Decay Class	Characteristics that determine decay class
1	Log is structurally intact, or mostly so; bark and branches still intact. Wood is not discoloured and there is little or no decay.
1.5	Log has some areas that are less intact than others; however, the bulk of the log is still structurally sound. Wood has begun to discolour and but there is still a significant amount of bark.
2	Structurally less intact but still hard, small branches are absent and little or no bark is left. Wood decay and/or discolouration is present, but in its infancy. Rotting of the surface of some of the exposed wood has begun.
2.5	A small amount of fibrous surface rot (FSR) is present and a large area of the log has significant discolouration. Log is still structurally intact but the wood has softened considerably. Some sub-surface pale rotten-wood types are present such as jelly and spongy rots.
3	Intermediate amount of decay but still supporting its own weight in most parts of the log. Hollow and soft in some places with cryptogams replacing bark. Almost all rotten-wood types can be found at this decay class in varying amounts. A mosaic of rotten-wood types, both pale and dark is present, representing parts of the log that is at early and late stages of decay. These include dark rotten-wood types such as dark fibrous surface rot, dark borer wood, gingerbread and dark cubic rot. Some areas contain the late stage rotten-wood type mudgut rot. Fibrous surface rot and discoloured wood are still present and meld into jelly and pocket rots on the sub-surface of the log.
3.5	The log only supports its weight in some areas. Moss roots and fungi have begun to invade a small part of the log. Like decay class 3, it contains a mosaic of rotten-wood types, but it differs because the darker ones are more prevalent and there is some formation of humus inside hollows of the log.
4	Does not support its own weight, wood decay is incipient and it may be hollow in parts. Some places may still be hard and log may be invaded by roots, moss and fungi.
4.5	Still some sign of original shape where middle has collapsed a mosaic of mudgut rot and humus is exposed. In drier areas some dark cubic rot is present and this is usually imbedded with roots which have almost invaded the entire log.
5	No sign of original shape, outer margins may remain visible but log almost completely decayed. Will be very soft in parts and is invaded by roots, fungi and moss.

Forest class 2001 (FC) is a coded system used by Forestry Tasmania to stratify forest types into classes that have broadly similar structural characteristics. *Forest class* was a variable that could describe many attributes of the forest. Each forest class is given its own number and is assigned to a broad forest class (Table 5.7). Five sites with identical or very similar forest classes were allocated to each broad forest class (Table 5.7). Without this table the ‘forest class’ partial dependence plots used to examine the contribution of the forest class variable in the BRT model is largely uninterpretable to a general audience. Table 5.7 should be referred to when examining the partial dependence plots in Section 5.3.4.

Forest regeneration age was categorised as young (1990s), middle age (1960–1990), old–middle-aged (1900–1960) and old (pre 1900s). Table 5.8 categorises height class and crown cover density used to discriminate between forest classes.

**Table 5.7 Broad forest class and corresponding forest classes, describing the structural attributes of each.**

Broad forest class	Forest class number	Description
Mature eucalypt forest without regrowth (MEFWoutRgro)	2	Old-growth forest dominated by rainforest element Very high mature eucalypt element with a high crown density Tall secondary species (non-eucalypt species) Low disturbance
Mature eucalypt forest with unheighted regrowth (MEFWURgro)	12, 13, 14	Wet sclerophyll forest Moderate-high mature eucalypt height with a high crown density Regrowth element from wildfire, varying age Moderately tall and dense regrowth Mixed-age regrowth element Low-moderate disturbance
Mature eucalypt with aged regeneration from partial logging (MEWARgen)	18, 20	Mainly wet sclerophyll but can be mixed forest Tall mature eucalypt element with low crown density Moderately high, middle-aged regeneration element Canopy density of eucalypt regeneration is high Moderate disturbance
Unaged eucalypt regrowth with mature eucalypt (URgroEWM)	22, 25, 26	Wet sclerophyll forest Mature eucalypt height is tall and crown density moderate-high Regrowth element old-middle-aged (deduced from fire history) Canopy density of regrowth is high Moderate disturbance
Pure unaged eucalypt regrowth (PURgroE)	34, 37, 38, 39	Mixed or wet sclerophyll forest No mature eucalypt element Regrowth is high, old-middle-aged, and canopy density moderate-high Secondary species have moderate –low height Moderate disturbance
Eucalypt regrowth with aged regeneration from partial logging: 1960-1979 (ERRWARgen)	54, 58	Wet sclerophyll and mixed forest Mature eucalypt element height is moderate-high, with a low canopy density Low-moderately tall, middle age regenerating eucalypt Canopy density of regenerating eucalypts is high Moderate disturbance
Eucalypt regrowth with aged regeneration from partial logging: 1980-1999 (ERRWARgen)	62, 66	Wet sclerophyll and mixed forest Mature element rare but when present is very tall Low-moderately tall, middle young age regenerating eucalypt Canopy density of regenerating eucalypts is low Moderate-high disturbance

**Table 5.8 Generalised characteristics of the eucalypt element derived from forest class used in the BRT and BGLM models.**

<b>Forest class description</b>	<b>Low</b>	<b>Moderate</b>	<b>High</b>
Density of mature eucalypt crown cover (%)	5–20	20–40	40–70
Density of regrowth eucalypt crown cover (%)	1–10	10–50	50–70
Height of mature eucalypt element (m)	1–34	34–55	55–76
Height of regrowth/regeneration eucalypt element (m)	1–27	27–37	37–50

### 5.2.4 Modelling procedures

Three modelling techniques, generalised linear modelling (GLM) (McCullagh and Nelder 1989), boosted regression trees (BRT) and boosted generalised linear models (BGLM), were used to explore whether the presence of beetles was influenced by the 15 CWD and 9 CWD-site attributes (see Table 5.3 and Table 5.4). Multiple modelling techniques were chosen to (i) test and compare model efficiency, (ii) accommodate the large number of combinations of data possible in this study (822 logs, three sub-plots in each log, 20 rotten-wood type categories, 14 different species of trees and six beetle species), and (iii) decrease the chance of overfitting (Shapire 2003).

Generalised linear models were fitted using CWD and CWD-site predictor variables but their outputs were much more complicated than what is presented below and they did not perform as well. For these reasons only the AUC results are presented for the BGLM. The models were also fitted without age of regeneration from 1990s and forest class taken out, but this made no difference to model performance. The results are therefore the best supported outcomes from a large number of exploratory model evaluations.

#### *Generalised Linear Model (GLM)*

Generalised linear modelling proceeded using a forward stepwise selection technique, which reduced the risk of over fitting. The starting model included only rotten-wood type as a predictor variable and presence/absences the dependent variable. All covariates were then added to the model (CWD and CWD site variables) and the change in fit assessed using likelihood ratio tests (based on changes in deviance of the two competing models).

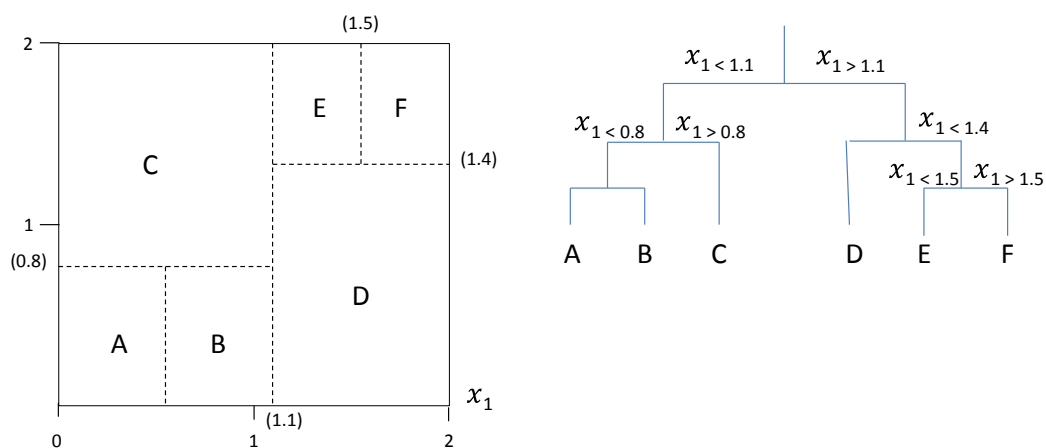


### *Regression trees*

Tree-based models partition the predictor space into hyper-rectangles that are a recursive subdivision of covariate space. They then fit the most probable constant to each region. Figure 5.2 shows a simple two dimensional example. The decision rules embodied by the tree (Figure 5.2, right) correspond to a recursive partitioning of the covariate space into rectangles (Figure 5.2, left). Within each rectangle the model fits a mean, so the fitted surface is constant within each rectangle and discontinuous across the edges. The partitioning itself is selected so that the response is as homogenous as possible within each rectangle.

The recursive subdivision or binary splitting creates ‘tree growth’, as it is repeatedly applied to its own output until the stopping criterion is reached. For non-boosted trees, the stopping criterion is set low, which builds huge trees which then have to be pruned. For boosted regression trees the criterion is set higher so branching tends to stop earlier. An effective strategy (and the one which was used in this study) is to ‘grow’ a large tree and then prune it by collapsing the weakest links, as identified using cross-validation (Breiman *et al.* 1984; Hastie *et al.* 2001; De’Ath 2007).

One great advantage of modelling using regression trees is that the results can be presented as a simple sequence of decision rules. Other advantages of this model include that any type of predictor variable can be used; the final model is not affected by monotone transformations or predictor variables that have different measurement scales; and poor performing predictor variables are seldom selected (Elith *et al.* 2008). In addition, regression trees are not sensitive to outliers and if predictor variables have missing data, surrogates are used (Breiman *et al.* 1984). They represent information that is intuitive and easy to visualise (Elith *et al.* 2008). De’ath and Fabricius (2000) give a good description of regression trees for ecological use.



**Figure 5.2** Simple design of the final output of a classification tree (right), showing two predictor variables, split at two points respectively  $> 1.1$  and  $< 1.1$ , and terminal nodes A - F (response variables). In the case of this study:  $> 1.1 = \text{tree species}$  and  $< 1.1 = \text{forest class}$ . A and D are the beetle species most likely to be found in CWD of a particular tree species or forest class (for example, A could equal *L. menalcas* and D could be *C. deplanata*). The decision rules embodied by the tree (right) correspond to a recursive partitioning of the covariate space into rectangles (left).

### Boosting

In this study, regression tree models were boosted to improve model accuracy.

Rather than finding a single highly accurate prediction rule (or single best fitting model), boosting identifies and averages the results from many competing models (Schapire 2003).

For boosted regression trees, many trees are fitted in sequence. The tree fitted in the first step is the tree that gives the best overall classification. Trees fitted in subsequent steps focus on residuals from the previous step, so that when applied in concert, the fitted trees outperform any single tree. Schapire (2003) provides a good overview on the boosting approach and its applications. Boosting is unusual in that by merging many simple classification rules, it automatically performs a forward stepwise procedure of model selection (Eilth *et al.* 2008).

In the present study overfitting was a potential problem because the number of predictor variables exceeded the number of sites (i.e. 35 sites and  $> 40$  predictor variables) and some descriptors were highly complex, using rotten-wood type categories as an example: the process of fitting the rotten-wood types is complicated by the large number of categories which increases the risk of overfitting. But their inclusion is justified because all rotten-wood types are recognisably different and cannot be pooled or re-categorised to decrease the terms used in the model. If they were to be pooled for example, pale vs. dark

rotten-wood types, this would make the models too general, potentially losing valuable ecological information.

#### *Boosted regression trees (BRT)*

Boosted regression trees were used to assess the influence of 15 CWD covariates (*diameter at intersect, volume of sample spot, rotten-wood type proportion* (proportion expressed as a percentage), *rotten-wood type, log length, decay class, log decay class, log off ground, log burnt, log cut, species present, adult or larva, number of individuals, tree species close to log end*), 9 CWD-site covariates (*age of regenerating forest, volume sampled, volume of dead wood (CWD), diameter sampled, Rgr, Rgen and Mat/Rgr, most recent fire, broad forest class, dominant eucalypt species, non-eucalypt species*) on species presence for each species separately, while protecting against the risk of overfitting. Producing a BRT is a technique that aims to improve the performance of a single model by fitting many models and combining them for prediction. BRT uses two algorithms: ‘regression trees’ from the classification and regression tree group of models, and ‘boosting’ which builds and combines a collection of models. For a discussion on the important features of BRT in an ecological context and a tutorial of the model see Elith *et al.* (2008) and Ridgeway (2006).

Because boosting produces hundreds and even thousands of decision trees the R ‘*gbmboost*’ package (Bühlmann and Hothorn 2007) was used to estimate the relative influence of each predictor variable. Model interpretation was further facilitated by the use of partial dependency functions, which show the effect of each influential predictor variable on the response after accounting for the effect of all other predictor variables in the model (Elith *et al.* 2008). Although these graphs may not be a perfect representation of effect sizes for each predictor variable because of correlations or interactions among them, they provide a useful basis for model interpretation (Elith *et al.* 2008; Friedman and Meulman 2003). Partial dependency functions were run for the top eight performing variables.

In R, the boosted regression tree statistical package is called ‘*gbmboost*’ but will be referred to as BRT in this thesis.

The boosting technique was also applied to the generalised linear models and from now on these models will be referred to as boosted generalised linear models

(BGLMs). The same predictor variables were used in the BGLMs (15 CWD variables and 9 CWD-site variables).

### 5.2.5 Validation of predictive models

Four methods were used to evaluate the performance of modelled beetle distributions: stepwise selection of predictor variables, Akaike Information Criterion (AIC), the area under the curve of the Receiver Operator Characteristic (ROC), and ten-fold cross validation. These methods were used in this study because they are relatively easy to compute and are widely used in predictive habitat modelling.

After the models were validated by using the above techniques the evaluation focused on predictive performance at sites based on species presence and in some of the BGLMs the predictive performance was based on the absence of species. In other words the model included predictor variables that predicted for a species absence at a particular site.

#### *Akaike Information Criterion (AIC)*

The AIC was used in this study to measure a models fit. The information theoretic measure Akaike's Information Criterion (Akaike 1978; Burnham and Anderson 2001), like stepwise selection, is a strategy for selecting predictor variables, defining the number of predictor variables by building several models and comparing them using the AIC. If all predictor variables exert some influence over the responses and larger sample sizes are capable of detecting and including more of these relationships then a model with the smallest AIC is best (Ramsey and Schafer 2002).

#### *The Area Under the Curve (AUC) of the Receiver Operator Characteristic (ROC)*

The efficiency of all models in this study was tested using the area under the curve (AUC) of the Receiver Operating Characteristic (ROC) to assess the agreement between the presence/absence records and predictions. The AUC has been used extensively in species distribution and predictive habitat modelling (Elith et al. 2006). It measures the ability of a model to discriminate between sites where a species is present or absent (Elith et al. 2006). Area under the curve is considered to be an effective indicator of predictive habitat model performance, independent of threshold probability at which the presence of the study species is accepted (Elith et al. 2006).

The ROC curve is obtained by plotting the probability of true presence (described as ‘sensitivity’) against the probability of predicting true absence (described as ‘specificity’) for all probability thresholds in the range 0 -1. The area under the curve represents model performance. An AUC score of 1 indicates perfect discrimination, a score of 0.5 implies predictive discrimination equivalent to a random guess and values <0.5 indicate a performance worse than random (Elith *et al.* 2006).

In this study, all models return, for each location, a probability that represents the likelihood that a given species will be found at that location. A location is then classified as ‘presence’ or ‘absence’ by comparing to a threshold probability. The chance of falsely classifying a location as a presence is reduced by increasing this threshold, at the expense of increasing the chance a location will be falsely classified as an absence. In other words, locations above the threshold predict for species presence and locations below predict for absences. In the case of this study it has the power to indicate how useful the models are at defining coarse woody debris (CWD) attributes that are important to each study species.

#### *k-fold cross validation*

The predictive performance of a boosted generalised linear model can be assessed through K-fold cross validation. The data are divided into k groups of points drawn at random, then each group is dropped in turn and predictions are made for the excluded group based on the fit of the model to the remaining data points. k-fold cross validation is similar to jack-knifing, the leave one out assessment (Osborne and Tigar 1992) but is computationally more efficient because the model needs to only be refitted to ‘k’ subsets of the data. By dropping more points the model creates a better reflection of its performance when using new data (Verbyla and Litvaitis 1989; Fielding and Bell 1997), this in turn creates a more robust model. In this study, the k-fold cross-validated model (i.e. prediction success) was assessed using the area under the curve (AUC) from the receiver operator characteristic (ROC) (Beck and Shultz 1986; Boyce *et al.* 2002).

For the abundance data, cross-validation was performed on a site by site basis. The data from each site were dropped in turn and predictions made for the excluded site, based on the fit of the model to the remaining sites. Cross

validating in this way provides a better test of how the model predictions will generalise to unseen sites.

All models were fitted in R (R Development Core Team 2006) version 2.8.1, using the following packages: *gbmboost*, *glm*, *glmboost* and *gam*. BRT and BGL models were used to predict the presence of the study species using CWD- and CWD-site predictor variables. The AIC and K-fold cross validation were used to test the validity of CWD-site predictive habitat models. Detailed explanations of these techniques are provided in (Section 5.2.5). In brief, the contribution of a particular variable that predicts variability in presence of a beetle is termed ‘relative influence’ and is presented as a percentage (Elith *et al.* 2008). The decision to discuss the predictor variables depended on their relative contribution to the model for both BRT and BGLM. In this study, only the top eight predictor variables (that is the eight predictor variables with the highest relative influence) were considered influential. To make the interpretation of each BRT model easier, partial dependence plots were developed for the eight most influential predictor variables.

### **5.2.6 Interpreting model output: partial dependence plots from BRT models**

The partial dependence plots shown in Figures 5.7a to 5.12b indicate which sub-category of predictor variable is driving the influential relationship between that variable and species presence that is revealed in the BRT analysis (shown in Table 5.13). For example, the BRT for *L. menalcas* included eight predictor variables, with MUD being the best performing (Table 5.13). While this is an interesting result the partial dependence plots provide more detail when interpreting this result. For example, the top left plot in Figure 5.7a can be interpreted as follows: at a sample-spot, if the proportion of rotten-wood type MUD was greater than 58% there was an increase in the probability of occurrence of *L. menalcas* (see line on plot spike and then increase as the proportion (%) of MUD increases). To give another example for the *Lissotes menalcas* BRT model output, the partial dependence plot for *forest class* predictor variable (top left hand plot, Figure 5.7b) presented a series of bars that align with each *forest class*. The bars on the plot vary in position depending on their influence, for example, the highest bar on the *forest class* partial dependence plot aligns with *forest class 38* and is interpreted

as follows: within the study area the probability of occurrence of *L. menalcas* increases at sites that are categorised as *forest class 38*.

### 5.3 Results

#### *Associations among rotten-wood types and species presence*

In total, 822 logs were sampled all at varying stages of decay and of various sizes (diameters ranged from 5 cm to >1m; lengths varied from 1m to >35 m). From these, 3237 beetles (adults and larvae) were collected over the 2.25 years of the study (see Table 5.9 for total counts).

**Table 5.9 Absolute abundance of the six study species.**

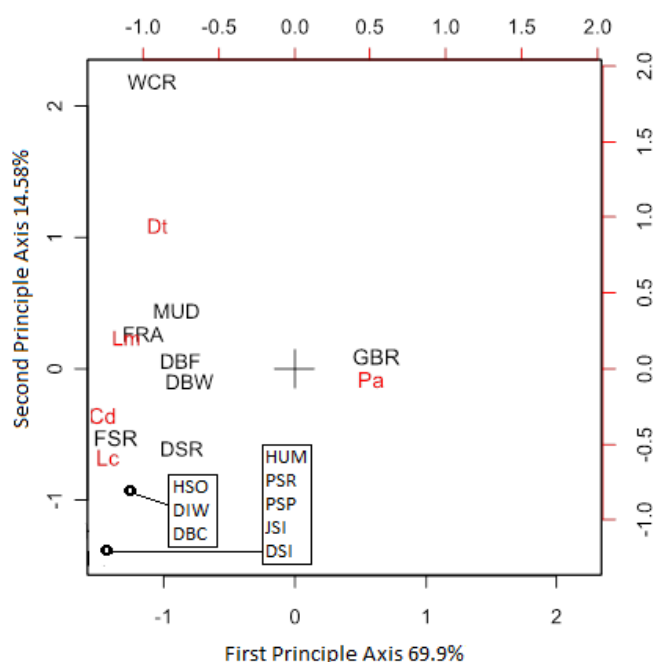
Species	Larva	Adult	Total
<i>Lissotes menalcas</i>	174	109	283
<i>Lissotes cancroides</i>	180	93	273
<i>Coripera deplanata</i>	307	15	322
<i>Prostomis atkinsoni</i>	1377	610	1987
<i>Dryophthorus</i> ECZ sp. 02	16	301	317
<i>Toxentes arcuatus</i>	52	3	55

#### 5.3.1 Results of the CA with count data

In general, both adults and larvae were found in the same rotten-wood types and the combination of adults and larvae showed a narrower rotten-wood type association than the adult-only analysis.

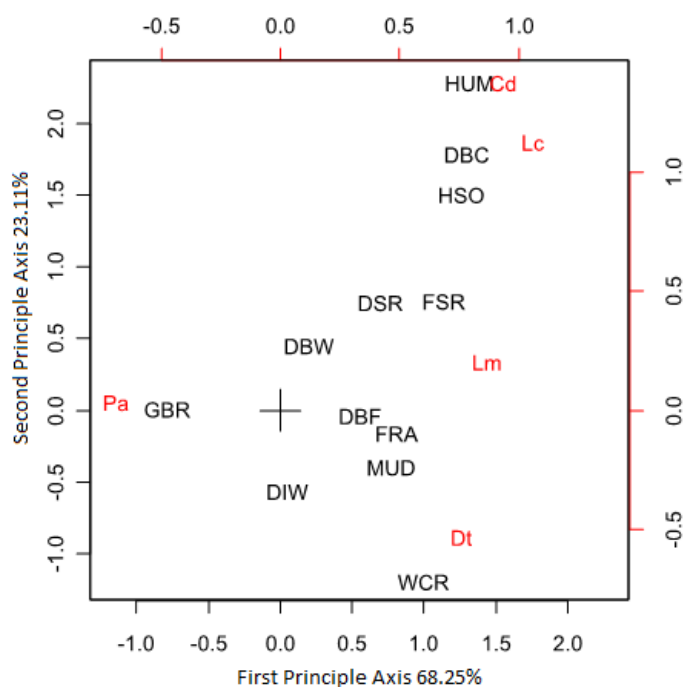
Results of the combined adult-larvae analyses revealed that, overall, saproxylic beetle species were either strongly associated with a single rotten-wood type, or associated with a suite of rotten-wood types, specifically the dark rotten-wood types (Table 5.10). Particular species were strongly associated with particular rotten-wood types. *Prostomis atkinsoni* was strongly associated with gingerbread rot (GBR), while *L. cancroides* and *C. deplanata* appeared to be associated with several rotten-wood types, including fibrous surface rot (FSR), dark brown cubic rot (DBC), humus-soil (HSO) and dark stringy rot (DSR; Figure 5.3). *Lissotes menalcas* was most closely associated with *T. arcuatus* frass (FRA) and mudguts (MUD), and less closely associated with dark brown fibrous (DBF) and dark borer wood (DBW; Figure 5.3). None of the species was associated with any of the pale rotten-wood types, pale string (PSR) or pale spongy rot (PSP), nor with incipient jelly and dark stringy rot (JSI and DSI).

Analyses of adult beetles in isolation revealed that they were associated with fewer rotten-wood types than were adults and larvae combined (compare Figure 5.3 with 5.4). As above, adult *P. atkinsoni* were again strongly associated with GBR (Figure 5.4). *Dryophthorus* ECZ sp. 02 meanwhile, were associated with wet cracks (WCR), while adult *L. cancroides* were associated with DBC and slightly further away, were equally distanced from HSO and HUM. Adult *L. menalcas* were associated with FSR, DSR and DBW (Figure 5.4). Adult *C. deplanata*, which were rarely found inside logs, were strongly associated only with humus (HUM), which was found outside logs that were in a late stage of decay (Figure 5.4).



**Figure 5.3** Factorial plan representation for the distribution of the adults and larvae (study species) according to rotten-wood type (based on count data). Distribution of the study species according to their rotten-wood types was obtained by the first and second principal axes. This plane represents 84.48% of the total information embedded in the original data matrix (tabulated count-data). Rotten-wood types are shown in black and beetle species in red. The analysis is based on total counts of adults and larvae at each sub-spot. Rotten-wood types: wet cracks (WCR), mudguts (MUD), frass (FRA), dark brown fibrous (DBF), dark borer wood (DBW), fibrous surface rot (FSR), dark stringy rot (DSR), gingerbread rot (GBR), humus-soil (HSO), discoloured wood (DIW), dark blocky crumbly (DBC), humus (HUM), pale spongy rot (PSP), pale stringy rot (PSR), jelly rot incipient (JSI) and dark stringy incipient (DSI). Species names: *Prostomis atkinsoni* (Pa), *Lissotes menalcas* (Lm), *Lissotes cancroides* (Lc), *Toxeutes arcuatus* (Ta), *Coripera deplanata* (Cd) and *Dryophthorus* ECZ sp 02.





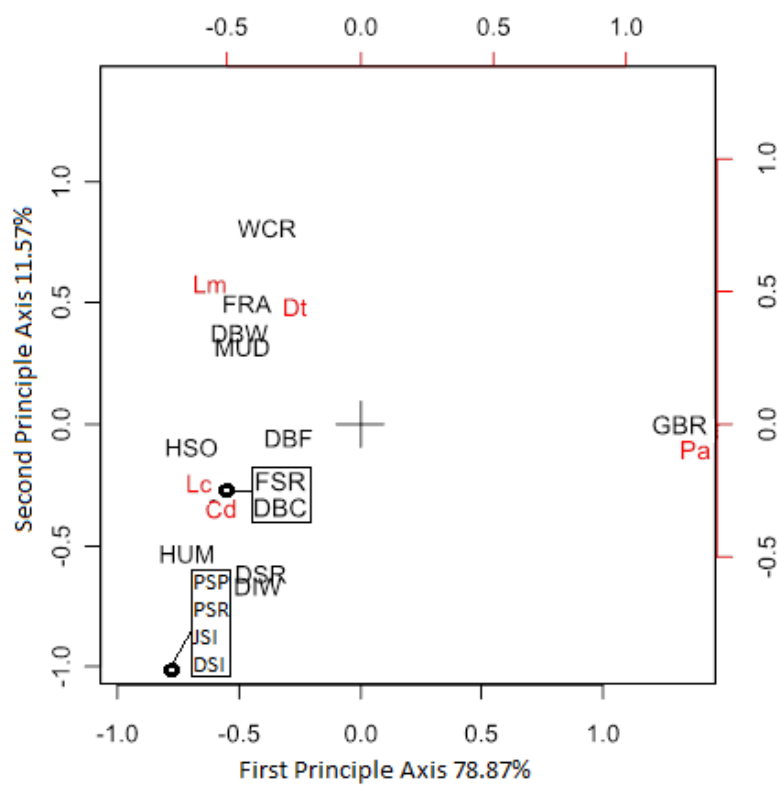
**Figure 5.4** Factorial plan representation for the distribution of the adult study species according to rotten-wood type (based on count data). Distribution of the study species according to their rotten-wood types was obtained by the first and second principle axes. This plane represents 91.36% of the total information embedded in the original data matrix (tabulated count-data). Rotten-wood types are shown in black and beetle species in red. The analysis is based on total counts of adults and larvae at each sub-spot. Rotten-wood types: wet cracks (WCR), mudguts (MUD), frass (FRA), dark brown fibrous (DBF), dark borer wood (DBW), fibrous surface rot (FSR), dark stringy rot (DSR), gingerbread rot (GBR), humus-soil (HSO), discoloured wood (DIW), dark blocky crumbly (DBC), humus (HUM), pale spongy rot (PSP), pale stringy rot (PSR), jelly rot incipient (JSI) and dark stringy incipient (DSI). Species names: *Prostomis atkinsoni* (Pa), *Lissotes menalcas* (Lm), *Lissotes cancroides* (Lc), *Toxeutes arcuatus* (Ta), *Coripera deplanata* (Cd) and *Dryophthorus* ECZ sp 02.

### 5.3.2 Results of the CA with incidence data

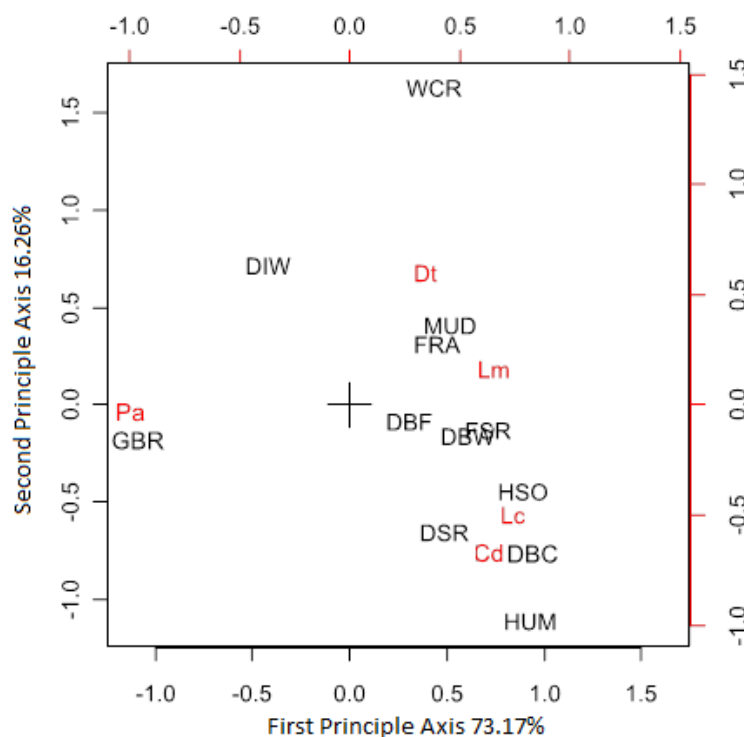
In general, the results of the correspondence analysis did not differ greatly when using incidence data as opposed to count data, with similar patterns of associations found for most species (Figure 5.5 and Figure 5.6). The main differences in these analyses were:

- *Prostomis atkinsoni* and *Dryophthorus* ECZ sp 02 were associated with a narrower range of rotten-wood types
- *Lissotes* species and *Coripera deplanata* were associated with a wider range of rotten-wood types
- *Lissotes menalcas* was associated most strongly with dark rotten-wood types and *Toxeutes arcuatus* frass.

The results of the count and incidence data do not differ greatly; this was possibly due to the strong association with the rotten-wood type regardless of count data or incidences of rotten-wood types.



**Figure 5.5** Factorial plan representation for the distribution of the incidence of the adults and larvae according to rotten-wood type. Distribution of the study species according to their rotten-wood types was obtained by the first and second principle axes. This plane represents 90.44% of the total information embedded in the original data matrix (tabulated count-data). Rotten-wood types are shown in black and beetle species in red. The analysis is based on total counts of adults and larvae at each sub-spot. Rotten-wood types: wet cracks (WCR), mudguts (MUD), frass (FRA), dark brown fibrous (DBF), dark borer wood (DBW), fibrous surface rot (FSR), dark stringy rot (DSR), gingerbread rot (GBR), humus-soil (HSO), discoloured wood (DIW), dark blocky crumbly (DBC), humus (HUM), pale spongy rot (PSP), pale stringy rot (PSR), jelly rot incipient (JSI) and dark stringy incipient (DSI). Species names: *Prostomis atkinsoni* (Pa), *Lissotes menalcas* (Lm), *Lissotes cancroides* (Lc), *Toxeutes arcuatus* (Ta), *Coripera deplanata* (Cd) and *Dryophthorus* ECZ sp 02.



**Figure 5.6** Factorial plan representation for the distribution of the adult study species at each sub-spot according to rotten-wood type. Distribution of the study species according to their rotten-wood types was obtained by the first and second principle axes. This plane represents 89.43% of the total information embedded in the original data matrix (tabulated count-data). Rotten-wood types are shown in black and beetle species in red. The analysis is based on total counts of adults and larvae at each sub-spot. Rotten-wood types: wet cracks (WCR), mudguts (MUD), frass (FRA), dark brown fibrous (DBF), dark borer wood (DBW), fibrous surface rot (FSR), dark stringy rot (DSR), gingerbread rot (GBR), humus-soil (HSO), discoloured wood (DIW), dark blocky crumbly (DBC), humus (HUM). Species names: *Prostomis atkinsoni* (Pa), *Lissotes menalcas* (Lm), *Lissotes cancroides* (Lc), *Toxeutes arcuatus* (Ta), *Coripera deplanata* (Cd) and *Dryophthorus* ECZ sp 02.

**Table 5.10** A summary of associations between study species and rotten-wood types based on counts ('+' = beetle associated with rotten-wood type and '0' = no association). Full names of rotten-wood types are provided in Table 5.1.

Study Species	MUD	DBW	DSR	DBF	GBR	DBC	HSO	WCR	FRA	DIW	FSR
<i>Lissotes menalcas</i>	+	+	+	+	0	0	0	0	+	0	0
<i>Lissotes cancroides</i>	0	+	0	+	0	+	+	0	0	+	+
<i>Coripera deplanata</i>	0	+	+	0	0	0	+	0	0	+	+
<i>Prostomis atkinsoni</i>	0	0	0	0	+	0	0	0	0	0	0
<i>Dryophthorus</i> ECZ sp. 02	+	0	0	0	0	0	0	+	0	0	0

### 5.3.3 The influence of log attributes on beetle presence: summary of model performance

Model performance was compared across the four modelling scenarios BRT, GLM (rotten-wood types only), GLM (rotten-wood types and CWD-site variables) and BGLM (Table 5.11). Both BGL models were included in the comparison of model performance to show that the model performed better with the addition of CWD-site variables. When the GLM is boosted (BGLM) the models still performed well and were easier to interpret than the GLM with the advantage of protection against overfitting. The plots for these models can be found in Appendix 5.2. For all species, the BRT performed the best, when using the AUC as an evaluation method for model performance (Table 5.11). All models performed well, with nearly all AUC values above 0.8 and in some instances, above 0.9, indicating that the habitat models for all species at the CWD level are very useful for predicting presence for each species. The worst performing models were fitted for *L. cancrroides* and models fitted for *P. atkinsoni* performed the best (Table 5.11).

For several models the mid-decay classes and dark rotten-wood types were most useful in predicting species presence. *Decay class 3* and *3.5* for example were included in BRT and BGLMs for several species (Table 5.12 and 5.13, Figure 5.7a and 5.8a) and dark borer wood (*DBW*) and mudguts (*MUD*) were some of the most influential rotten-wood type predictor variables for several species in the BRT and BGLMs (Table 5.12 and 5.13). *Forest class* and *decay class* predictor variables dominated in both the BRT and the BGLM for most species (Table 5.12 and 5.13). However, the BGLMs were generally more complex (Table 5.12 and Appendix 5.2), containing more predictor variables in the habitat models and the variables were often species specific, while the BRT provided a simpler model with fewer descriptors needed to perform well (Table 5.13). Consequently, the BRT model was the best model for predicting the incidence of the study species. The ecological interpretation of the BRT and BGLMs are discussed in Section 5.4 and summarised in Section 7.1, Chapter 7.

**Table 5.11 Comparison of model performance based on the area under the curve (AUC) of the receiver operating characteristics (ROC) plots. An AUC with a value of 1 is a model with perfect fit.**

Model	<i>Prostomis atkinsoni</i>	<i>Lissotes menalcas</i>	<i>Lissotes cancroides</i>	<i>Coripera deplanata</i>	<i>Toxentes arcuatus</i>	<i>Dryophthorus ECZ sp. 02</i>
BRT	0.94	0.89	0.81	0.85	0.88	0.94
GLM rot only	0.92	0.84	0.72	0.81	0.82	0.85
GLM rot + site	0.93	0.88	0.79	0.84	0.87	0.93
BGLM	0.92	0.85	0.77	0.82	0.87	0.84

### 5.3.4 Species incidence and habitat modelling

The results of this study demonstrate that CWD rotten-wood type is the primary determinant of the presence of saproxylic beetles, particularly dark rotten-wood types. All beetles showed a bias towards dark rotten-wood types in the BGLM (Table 5.12). In the BRT four out of six study species were found most frequently in mudguts and dark borer wood, and probability of occurrence increased when mudguts was present at >60% in a sample-spot and dark borer wood was >10% (Table 5.13, e.g. *MUD* and *DBW* plots in Figure 5.7a, 5.8b, 5.8a, 5.9b, 5.10a 5.10b). In contrast, only one of the beetles, *T. arcuatus*, was predicted to occur in pale rotten-wood types. Separation of species was largely seen in relation to proportion of dark rotten-wood types occurring at a sample-spot (rotten-wood plots in Figure 5.7a-5.12b).

The study species had marked association with dead wood with respect to its decay class. For the BGLM all species showed a bias towards intermediate decay classes, as did five out of the six species in the BRT (Table 5.12 and 5.13). Some species were able to exploit a wider range of decay classes than others (e.g. *L. cancroides* and *L. menalcas*). All species, (with the exception of *T. arcuatus*) most frequently occurred in *decay class* 3.5 (Table 5.12 and 5.13).

All species were found in the majority of forest classes but the probability of occurrence differed (bars aligned to forest classes in partial dependence plots in Figure 5.7b, 5.8a, 5.9a, 5.11b and 5.12a - the higher the bar the higher the probability of the species occurring in that particular forest class), most notable in the BGLM (Table 5.12). Many species were found more frequently in a group of

forest classes. For example, probability of occurrence is increased at sites with a *forest class of 34 and 54*. Forests defined by these forest classes are wet eucalypt or mixed forest with a minor mature eucalypt component (Table 5.7). The regrowth (after timber harvesting) is moderately tall, middle-aged and dense, often with a scrubby (trees <15 m tall) undergrowth (refer to Table 5.7 and 5.8). *Forest class* contributed more to the models than *broad forest class*, indicating that there was a finer scale of detail needed when describing habitat requirements; broader CWD-site elements in the *broad forest class* predictor variable were too general to make a better contribution than *forest class*.

The predictor variable *age of regeneration* was strongly associated with a higher probability of occurrence for several species. Most species were likely to be found in the older forests where age of regenerating forest is from early or pre- 1900s. However, many species showed a marked bias towards age of regenerating forest from the late 1970s and early 1980s, where partial logging occurred (*age of regen* plots from Figures 5.8 - 5.11). In contrast, the BGLM indicated that three species frequently occurred in young regeneration (1990s regenerating forest, Table 5.12 and *age of regen* plots in Figure 5.8 - 5.11).

The BGLM also included predictor variables that predicted absence for three species (Table 5.14). The variable that predicted absence for all species was no rot, indicating that a rotten-wood type must be present for these species to inhabit a sample-spot. However, a pale rotten-wood type is thought to significantly decrease the probability of occurrence of *L. cancroides* (Table 5.14). Predictor variables of absence were diverse and more emphasis was placed on variables that predict for presence. Preferences in relation to less important variables that predict presence were also diverse, particularly in the BGLM (Table 5.12). Their contribution to predicting the presence of species varied but was generally poorer than other predictor variables included in the model. The CWD descriptors *log decay class*, *volume of CWD*, *burnt* and *tree species* all contributed to the model's performance for only one or two species, (Table 5.12 and 5.13). All species were most commonly found in eucalypt CWD due to its dominance on the forest floor. In contrast, two species showed marked occurrence in the environment based on the dead wood of non-eucalypt tree species. For example in the *tree species* partial dependence plot in Figure 5.7b the highest bar in the plot aligns with *Acacia melanoxylon*, this suggests that the probability of *L. menalcas* occurring is

increased in the dead wood of *A. melanoxylon*. In Figure 5.12a, the *tree species* partial dependence plot indicated that *T. arcuatus* is found most frequently in *Acacia dealbata* (see also Table 5.12). These tree species are typical in wet sclerophyll forests of southern Tasmania.

**Table 5.12 Average contribution (AIC derived) of the most important predictor variables for BGLMs relating the presence of the six study species to CWD- and CWD-site model environment. Within-species ranked performance of predictor variables are indicated in brackets ('0' indicates a predictor variable that performed poorly and therefore not chosen in the BGLM)**

Predictor variable	<i>Lissotes menalcas</i>	<i>Lissotes cancroides</i>	<i>Coripera deplanata</i>	<i>Prostomis atkinsoni</i>	<i>Dryophthorus ECZ sp 02</i>	<i>Toxeutes arcuatus</i>
Forest class 38	0	0.071 (6)	0	0	0	0
Forest class 13	0	0.103 (8)	0	0	0	0
Forest class 37	0	0	0	0	0	0
Forest class 54	0	0	0.093 (5)	0	0	0
Forest class 58	0	0	0	0.303 (7)	0	0
Broad forest class PURgroE	0.260 (11)	0	0	0	0	0
Decay class 3	0.064 (9)	0.116 (9)	0	0.047 (4)	0	0
Decay class 3.5	0.032 (8)	0.275 (11)	0.149 (7)	0	0.206 (5)	0
Decay class 2.5	0	0.020 (3)	0	0	0	0
Decay class 4	0	0	0	0	0.111 (3)	0
Log decay class 4.5	0	0.051 (5)	0	0	0	0
Log decay class 4	0	0.080 (7)	0	0	0	0
Dark borer wood (DBW)	0.014 (6)	0.002 (1)	0.007 (2)	0.005 (1)	0	0.003 (2)
Mudguts (MUD)	0.012 (5)	0	0.005 (1)	0	0.007 (1)	0
Gingerbread rot (GBR)	0.006 (4)	0	0.007 (2)	0.037 (3)	0	0
Dark brown fibrous (DBF)	0.002 (3)	0.003 (2)	0.008 (4)	0.009 (2)	0.007 (1)	0
<i>Toxeutes arcuatus</i> frass (FRA)	0.001 (2)	0	0	0	0	0.025 (3)
Dark stringy rot (DSR)	0	0	0.005 (1)	0	0	0.025 (3)
Pale stringy rot (PSR)	0	0	0	0	0	0.001 (1)
Age of regenerating forest 1996	0	0	0.388 (8)	0.213 (6)	0.500 (6)	0
Age of regenerating forest 1979	0	0	0	0.065 (5)	0	0
Age of regenerating forest 1983	0	0	0	0	0.117 (4)	0
Age of regenerating forest 1934	0.018 (7)	0	0	0	0	0
Tree species <i>Acacia melanoxylon</i>	0.292 (12)	0	0	0	0	0
Tree species <i>Acacia dealbata</i>	0	0	0	0	0	0.174 (4)
Dominant eucalypt <i>E. regnans</i> with <i>E. obliqua</i>	0.106 (10)	0	0	0	0	0
Non eucalypt element (scrub <15m tall)	0	0.022 (4)	0	0	0	0
Non eucalypt element (teatree scrub)	0	0.148 (10)	0	0	0	0
Mature crown density 5	0	0	0.112 (6)	0	0	0
Volume sampled (cm <sup>3</sup> )	4.8e <sup>07</sup> (1)	0	0	0	0	0
Burnt	0	0	0.075 (3)	0	0.070 (2)	0

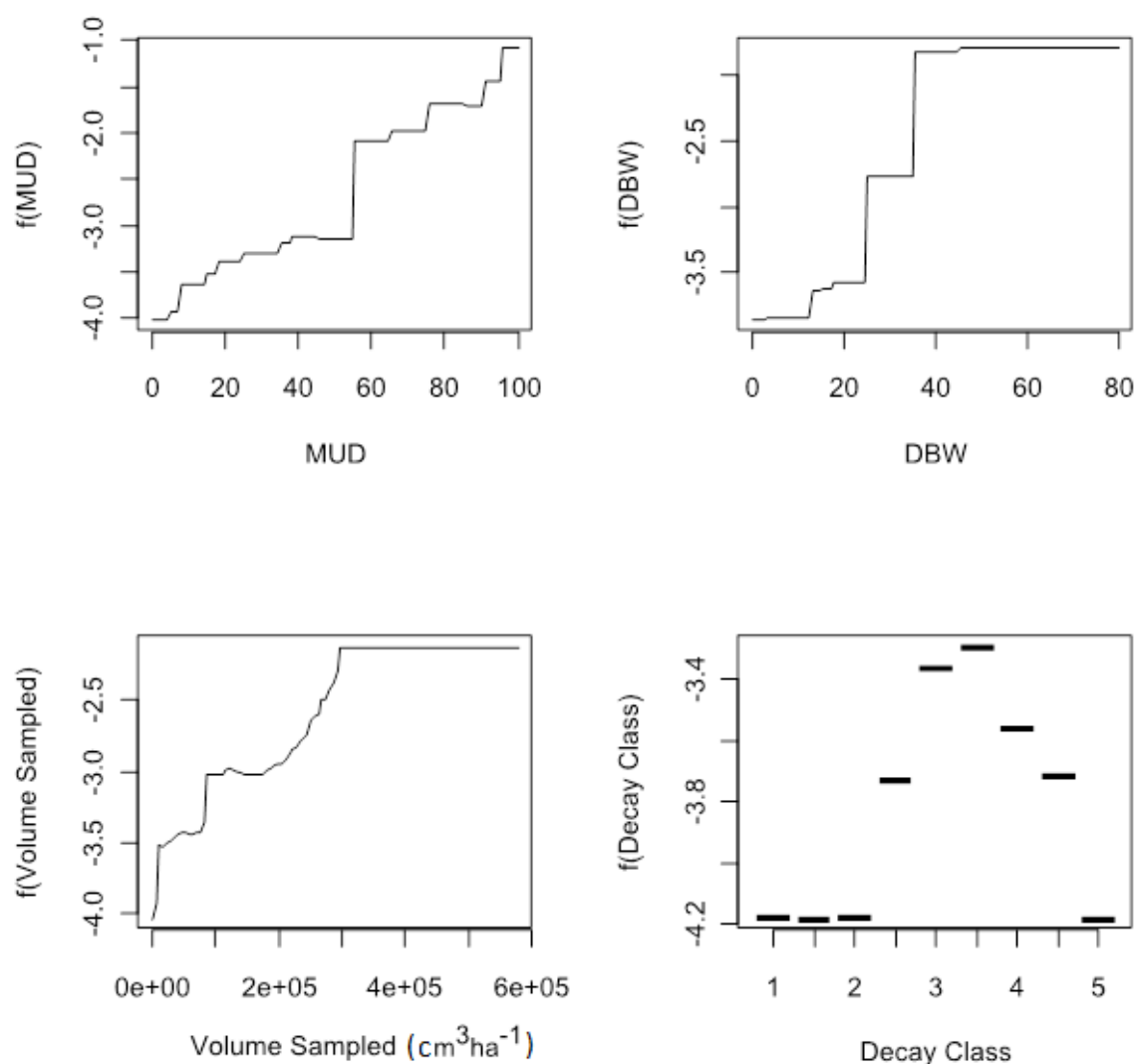


**Table 5.13** The eight most important predictor variables for the BRT models (number in brackets from 1-8) relating to presence of the study species to dead wood habitat at the CWD- and CWD-site scale . Values in brackets indicate within-species performance of each predictor variable ('0' indicates a predictor variable that was included in the analysis but performed poorly and therefore not chosen in the final model).

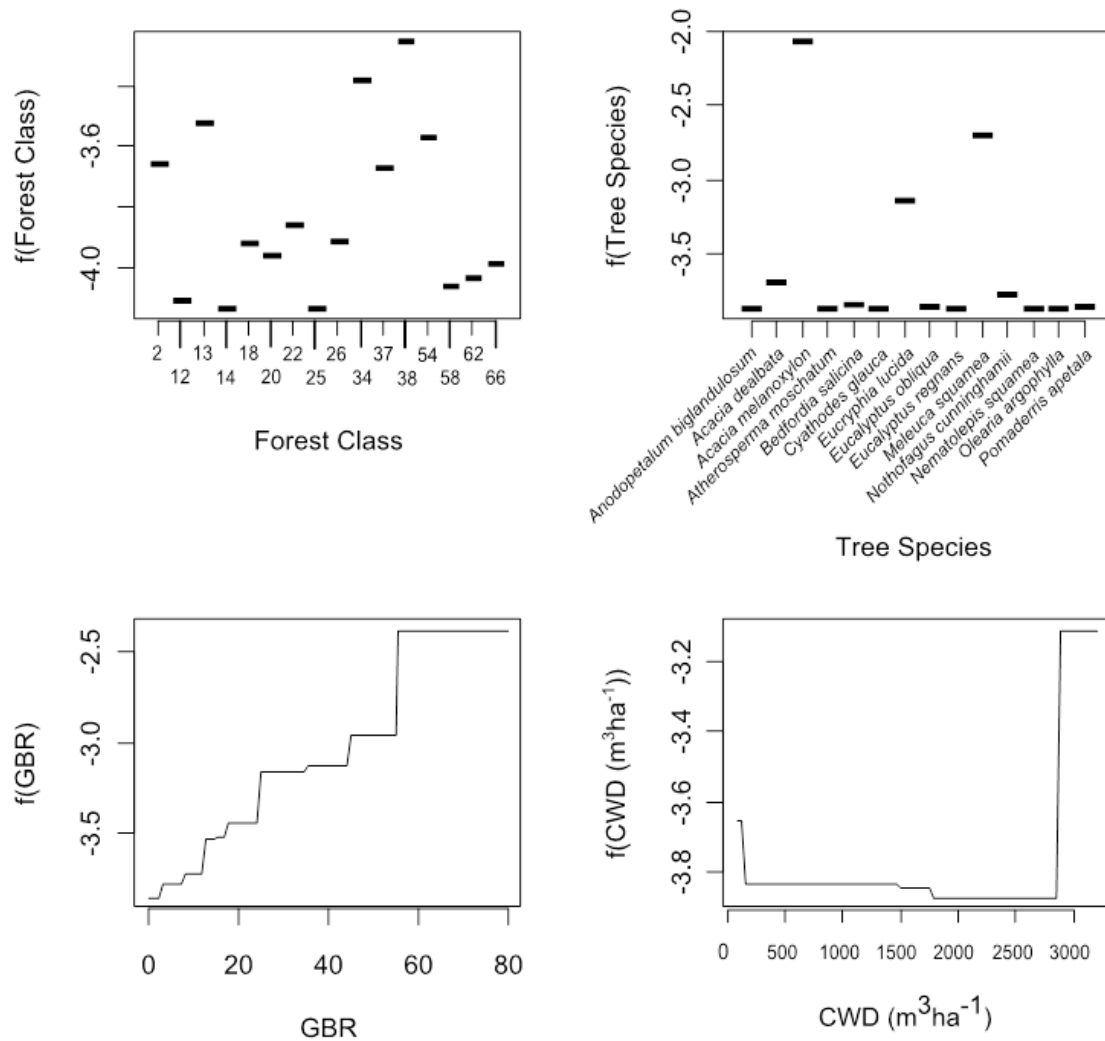
Predictor variable	<i>Lissotes menalcas</i>	<i>Lissotes cancroides</i>	<i>Coripera deplanata</i>	<i>Prostomis atkinsoni</i>	<i>Dryophthorus</i> ECZ sp. 02	<i>Toxeutes arcuatus</i>
MUD	25.74 (1)	4.00 (8)	12.06 (2)	1.93 (6)	17.83 (1)	0
DBW	15.18 (2)	4.64 (7)	6.50 (8)	4.11 (4)	0	16.34 (2)
GBR	5.25 (7)	0	0	68.71 (1)	6.55 (6)	0
DBF	0	7.11 (6)	22.48 (1)	11.55 (2)	14.33 (3)	0
DSR	0	0	7.39 (5)	1.81 (7)	0	3.76 (7)
FRA	0	0	0	0	2.08 (8)	55.23 (1)
PSR	0	0	0	0	0	4.67 (4)
PSP		0	0	0	0	4.08 (6)
DIW	0	0	0	0	0	4.36 (5)
Decay class	9.51 (3)	22.72 (1)	7.78 (4)	1.71 (8)	8.50 (5)	0
Volume sampled (cm <sup>3</sup> )	7.19 (4)	7.16 (5)	7.37 (6)	2.33 (5)	8.95 (4)	0
Forest class	5.69 (5)	14.50 (2)	7.28 (7)	0	2.69 (7)	3.76 (7)
Tree species	5.65 (6)	0	0	0	0	4.91 (3)
CWD m <sup>3</sup> ha <sup>-1</sup>	4.88 (8)	0	0	0	0	0
Log decay class	0	10.45 (3)	0	0	0	0
Age of regenerating forest	0	8.78 (4)	9.80 (3)	4.19 (3)	31.95 (1)	0

**Table 5.14** Average contribution (AIC derived) of the most important predictor variables for BGLMs relating the absence of the six study species to CWD- and CWD-site environment. Within-species ranked performance of predictor variables are indicated in brackets ('0' indicates a predictor variable that was not included in the BGLM because it performed poorly with other predictor variables outperforming this variable).

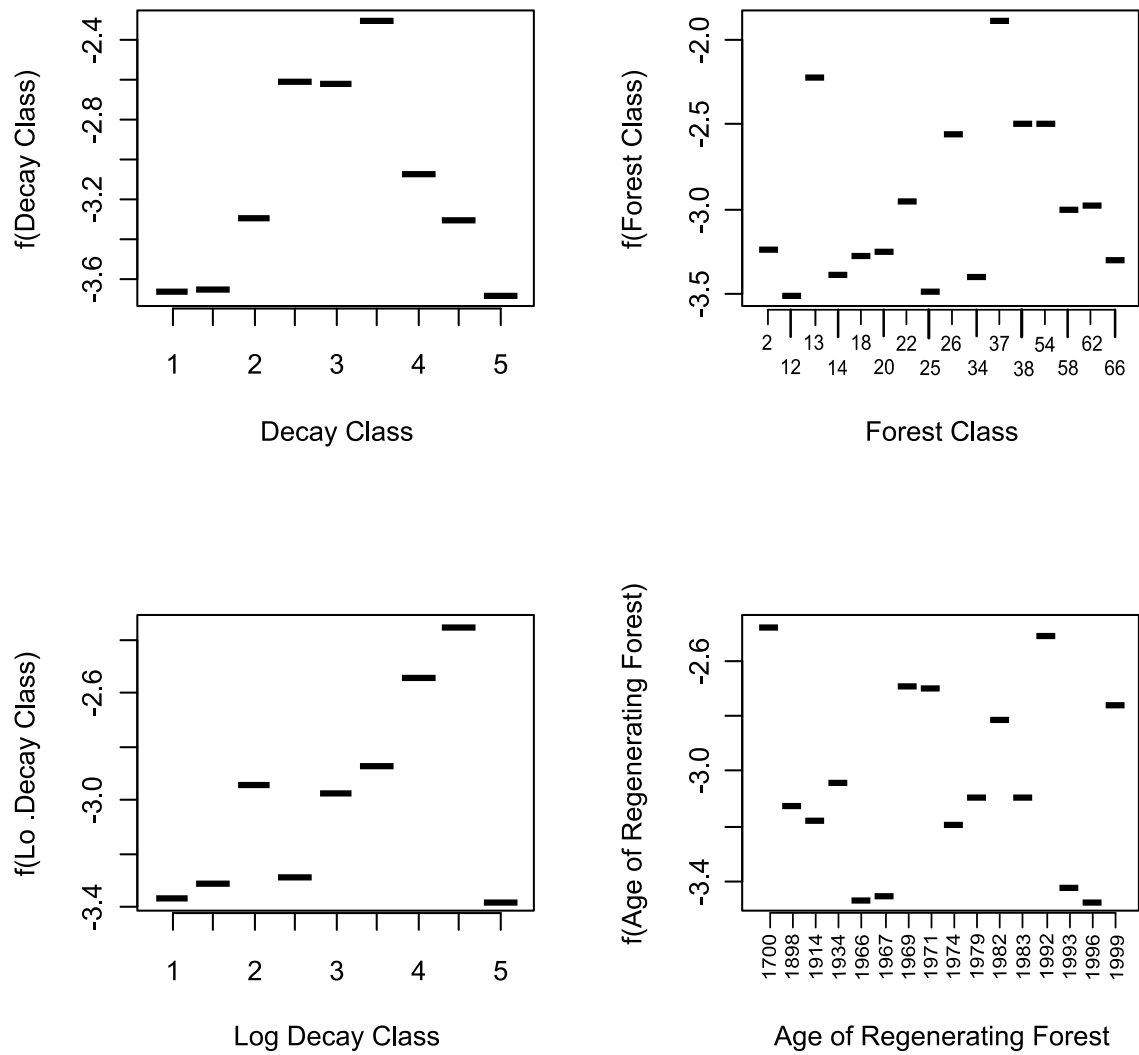
Predictor variable	<i>Lissotes menalcas</i>	<i>Lissotes cancroides</i>	<i>Coripera deplanata</i>
Mature height class 41-55m	-0.025 (2)	0	0
No rot (NOR)	-0.001 (1)	-0.005 (2)	-0.002 (1)
Pale stringy rot (PSR)	0	-0.001 (1)	0
Most recent fire 1966-1967	0	-0.008 (3)	0
Dominant eucalypt pure <i>E. regnans</i>	0	-0.030 (4)	0
Decay class 5	0	-0.867 (7)	0
Mature and regrowth	0	-0.071 (6)	0
Discoloured wood (DIW)	0	-0.001 (1)	0
Log decay class 5	0	-0.065 (5)	0



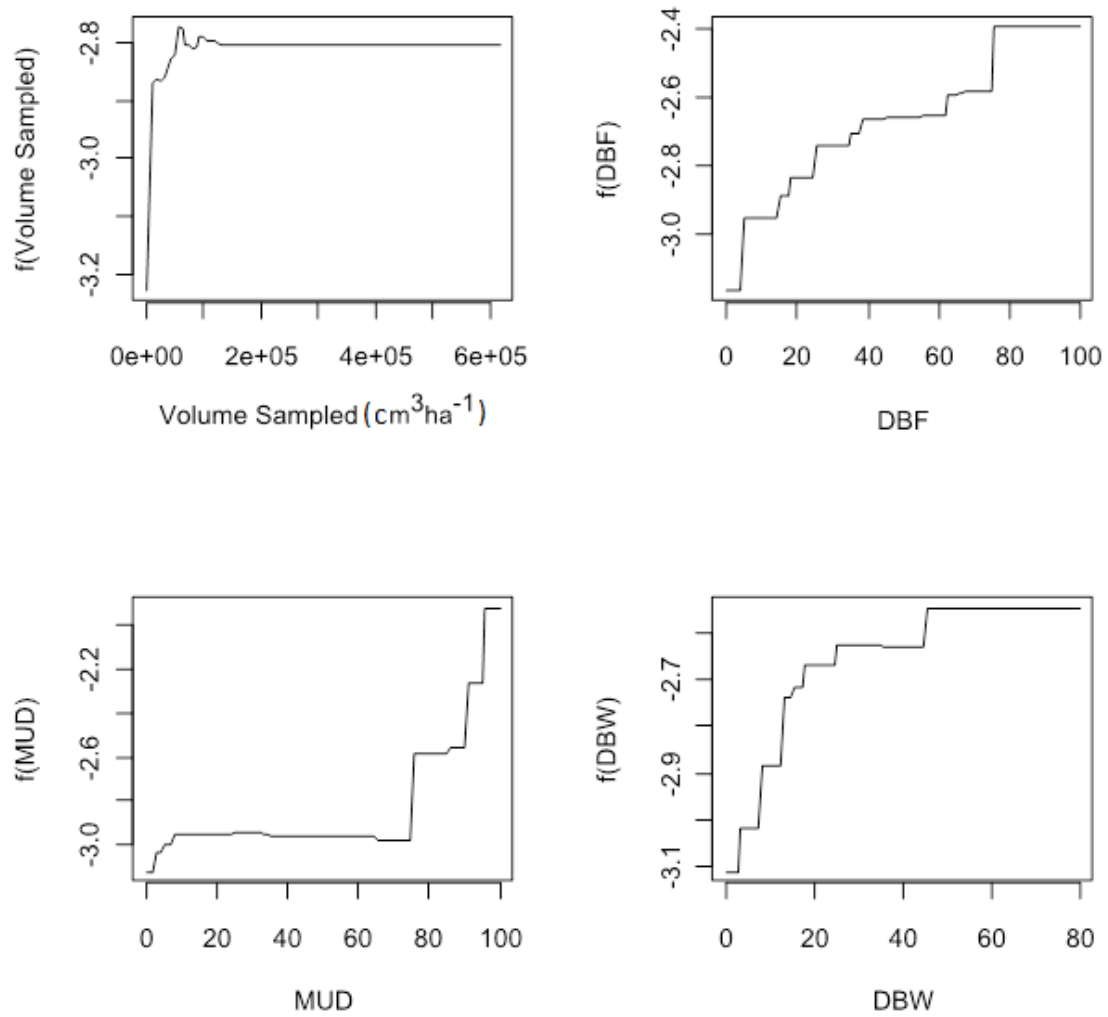
**Figure 5.7a** Functions fitted for the four most influential predictor variables in the boosted regression tree model (BRT) relating the probability of occurrence of *Lissotes menalcas* to its CWD environment. Rotten-wood type variables (MUD and DBW) are proportions expressed as a percentage. See Table 5.2 for rotten-wood types, Table 5.3 for CWD variables and Table 5.4 for an explanation of CWD-site variables. The probability of species occurrence increases with the increasing height of a bar or line on the plot. For example the partial dependence plot for MUD shows the line on the plot steadily increases and spikes at approximately 58, which means that the probability of occurrence of *L. menalcas* is thought to increase when the proportion (%) of MUD in a sample-spot is 58% or greater.



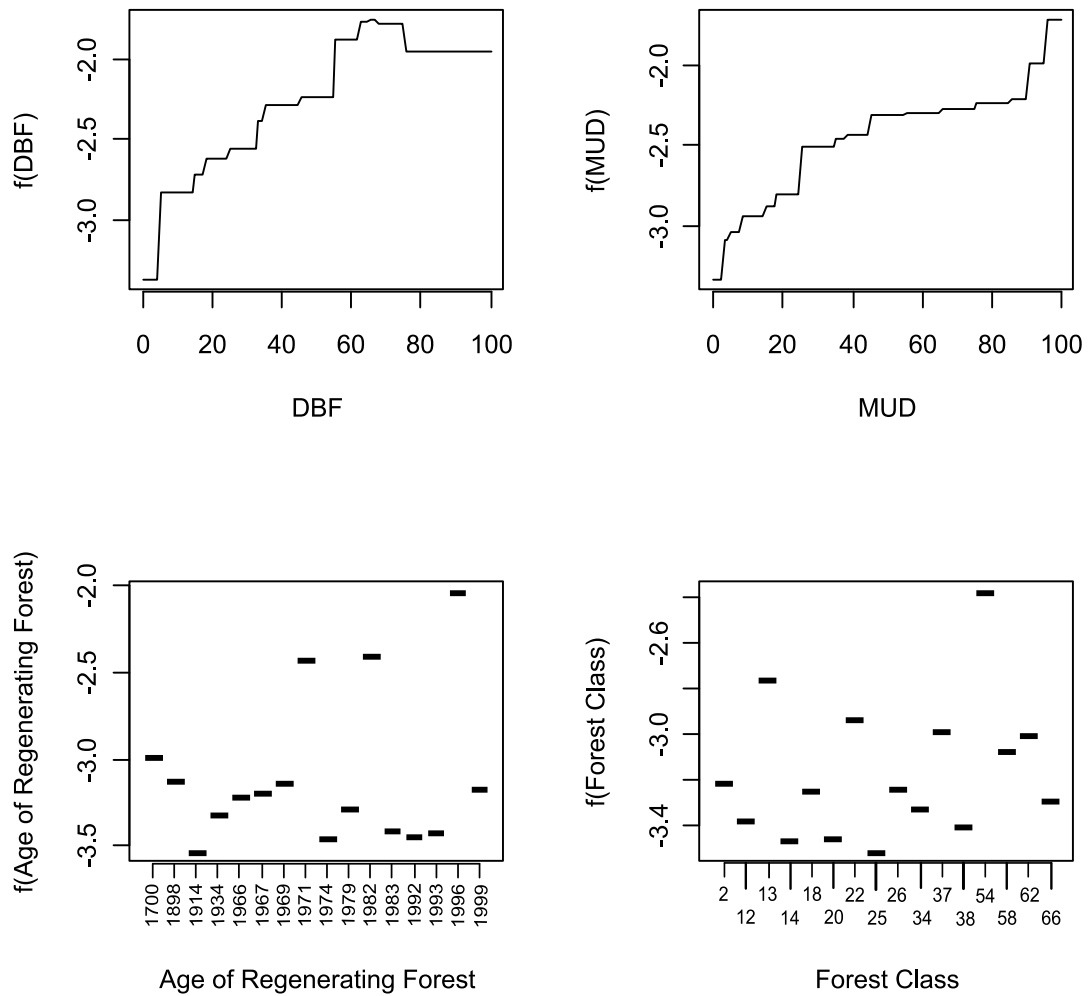
**Figure 5.7b** Functions fitted for the four most influential predictor variables in the boosted regression tree model (BRT) relating the probability of occurrence of *Lissotes menalcas* to its CWD environment. See Table 5.2 for rotten-wood types, Table 5.3 for CWD variables and Table 5.4 for an explanation of CWD-site variables. Table 5.7 explains the habitat attributes of each forest class (see forest class plot, top left). The probability of species occurrence increases with the increasing height of a bar or line on the plot.



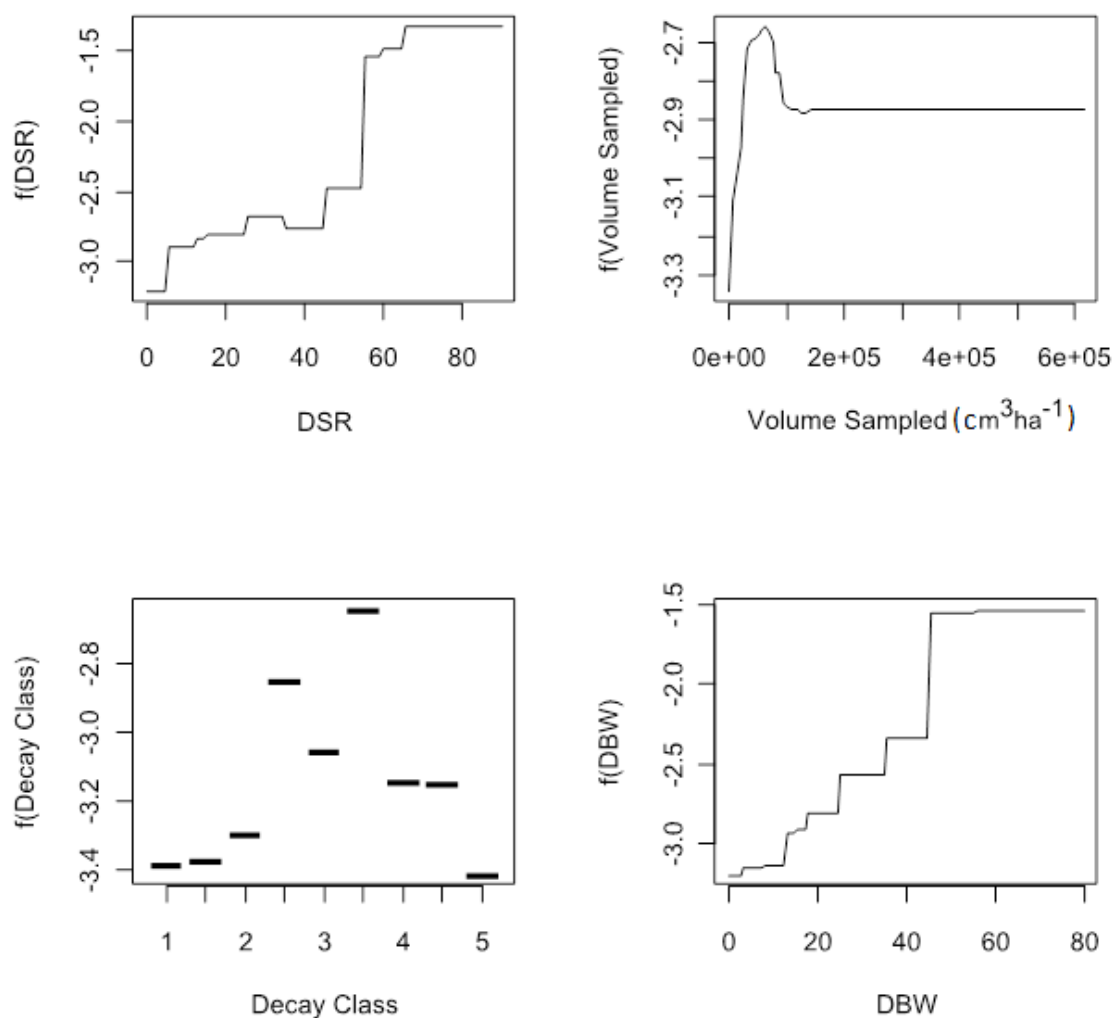
**Figure 5.8a Functions fitted for the four most influential predictor variables in the boosted regression tree model (BRT) relating the probability of occurrence of *Lissotes cancröides* to its CWD environment. See Table 5.2 for rotten-wood types, Table 5.3 for CWD variables and Table 5.4 for an explanation of CWD-site variables. Table 5.7 explains the habitat attributes of each forest class (see forest class plot, top right). The probability of species occurrence increases with the increasing height of a bar or line on the plot.**



**Figure 5b** Functions fitted for the four most influential predictor variables in the boosted regression tree model (BRT) relating the probability of occurrence of *Lissotes cancroides* to its CWD environment. See Table 5.2 for rotten-wood types, Table 5.3 for CWD variables and Table 5.4 for an explanation of CWD-site variables. The probability of species occurrence increases with the increasing height of a bar or line on the plot.

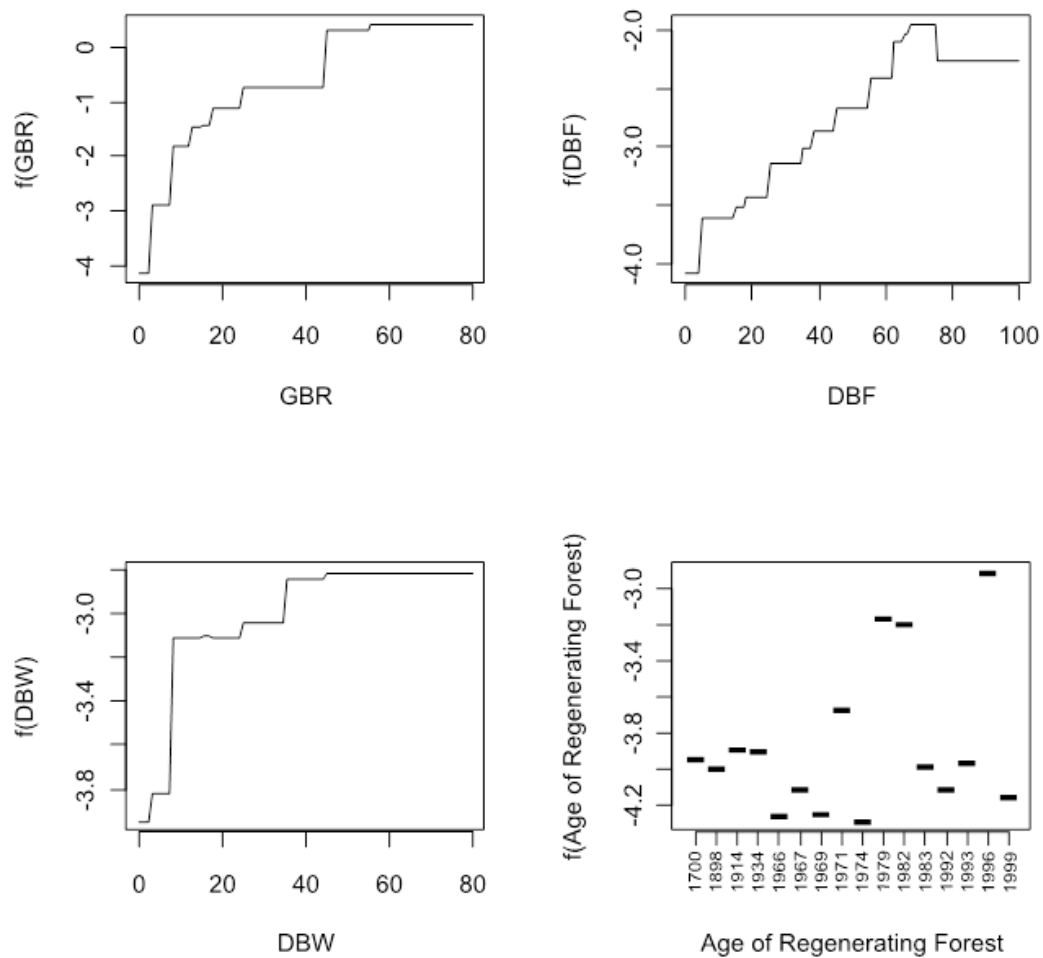


**Figure 5.9a** Functions fitted for the four most influential predictor variables in the boosted regression tree model (BRT) relating the probability of occurrence of *Coripera deplanata* to its CWD environment. See Table 5.2 for rotten-wood types, Table 5.3 for CWD variables and Table 5.4 for an explanation of CWD-site variables. Table 5.7 explains the habitat attributes of each forest class (see forest class plot, bottom left). The probability of species occurrence increases with the increasing height of a bar or line on the plot.

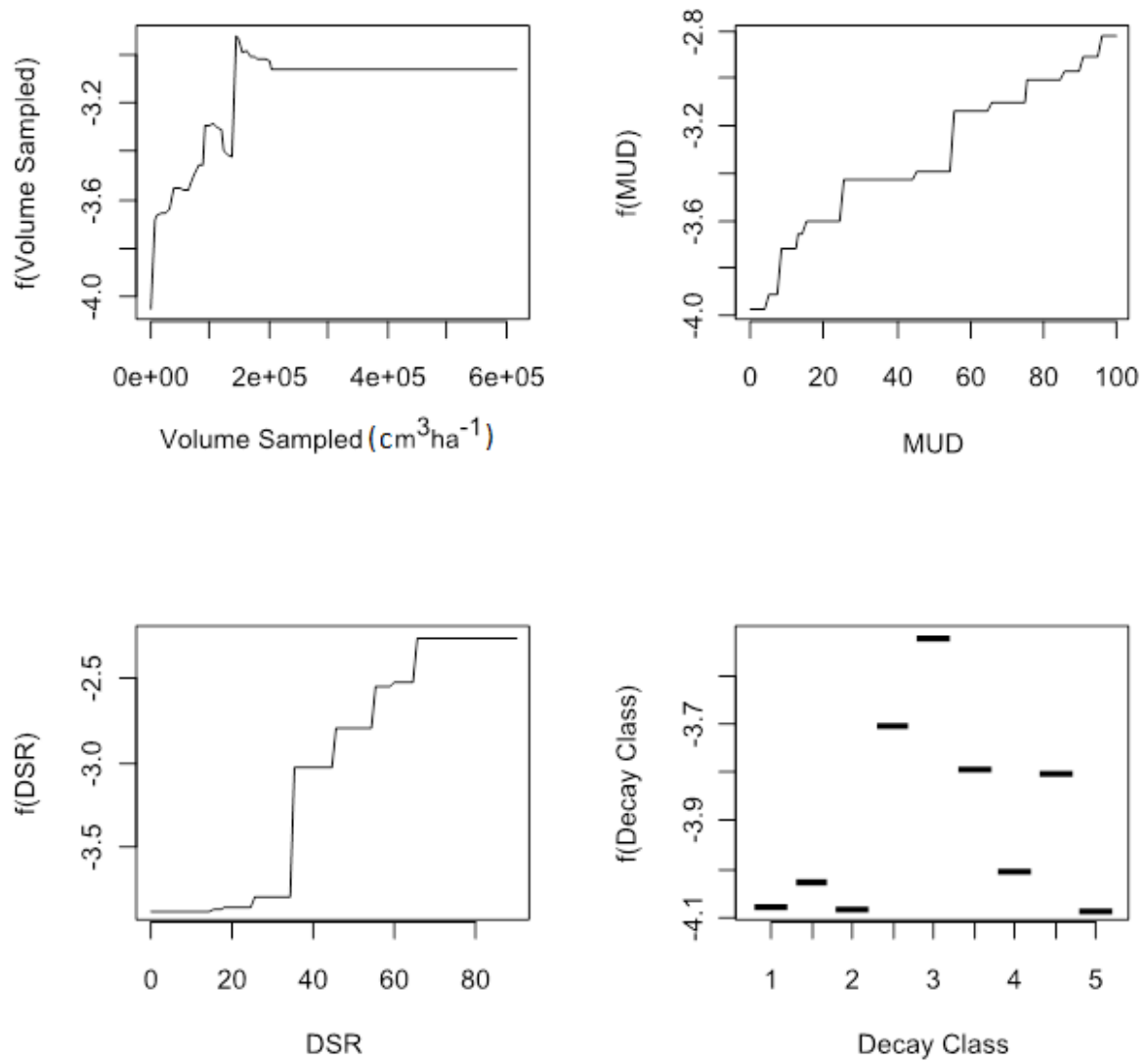


**Figure 5.9b** Functions fitted for the four most influential predictor variables in the boosted regression tree model (BRT) relating the probability of occurrence of *Coripera deplanata* to its CWD environment. See Table 5.2 for rotten-wood types, Table 5.3 for CWD variables and Table 5.4 for an explanation of CWD-site variables. The probability of species occurrence increases with the increasing height of a bar or line on the plot.

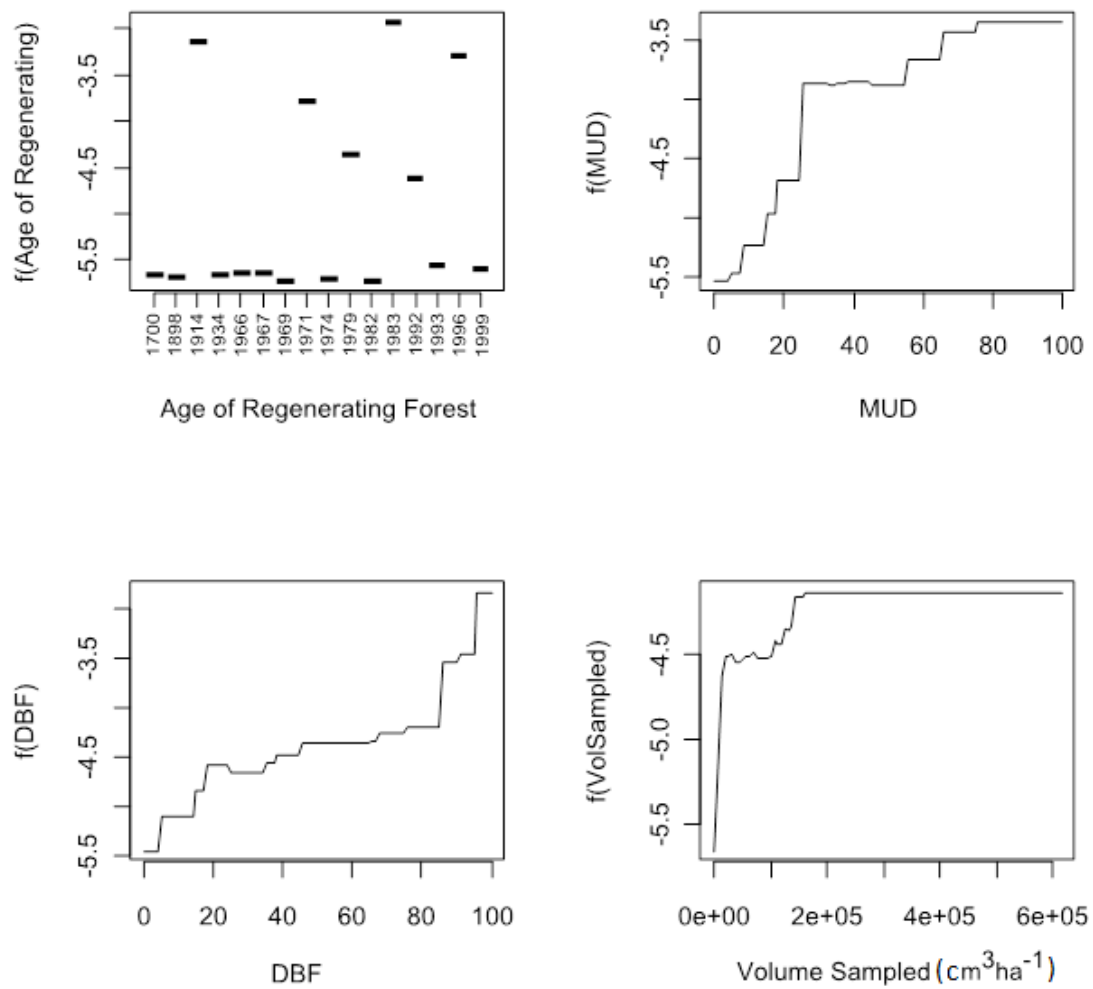




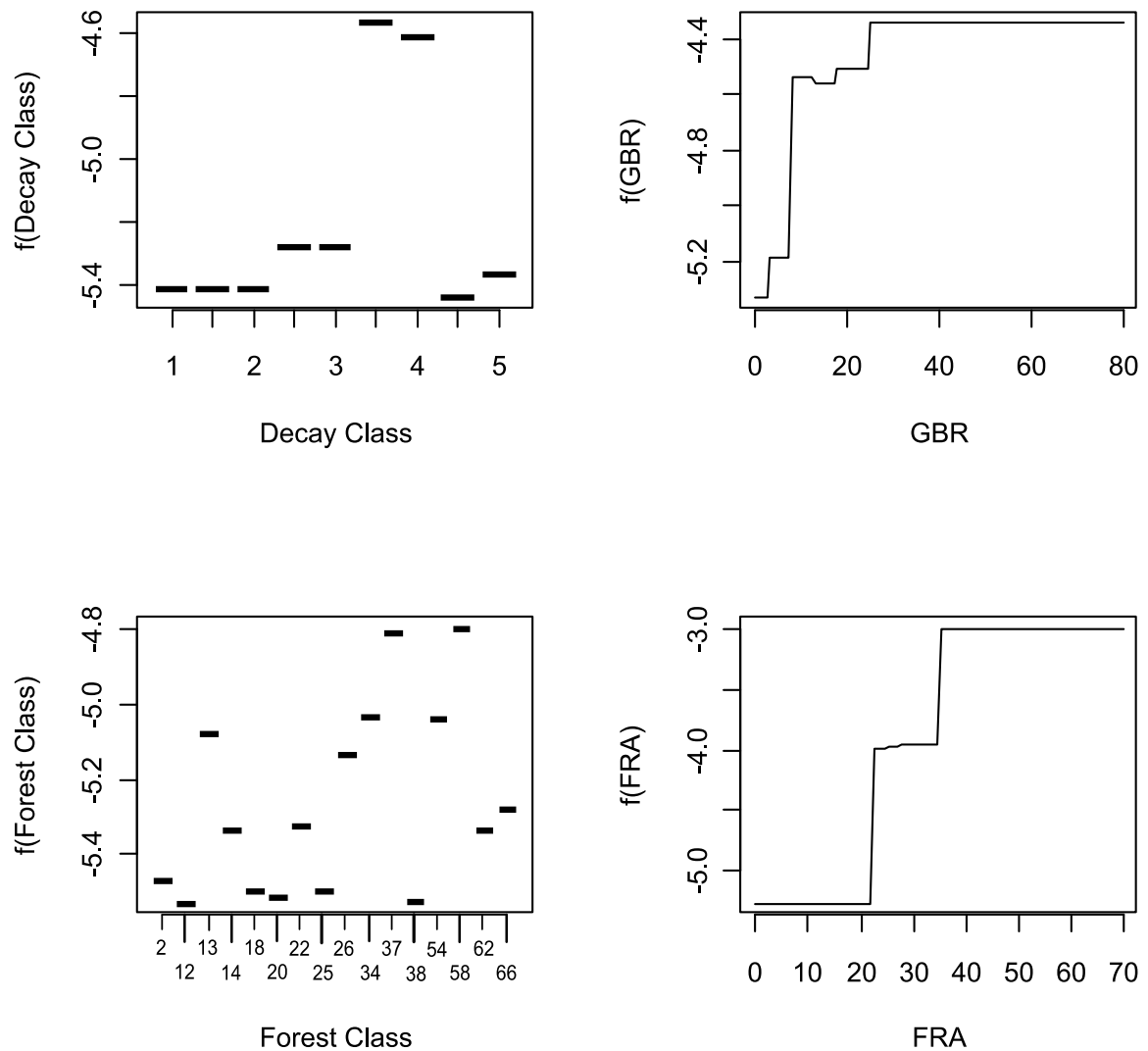
**Figure 5.10a** Functions fitted for the four most influential predictor variables in the boosted regression tree model (BRT) relating the probability of occurrence of *Prostomis atkinsoni* to its CWD environment. See Table 5.2 for rotten-wood types, Table 5.3 for CWD variables and Table 5.4 for an explanation of CWD-site variables. The probability of species occurrence increases with the increasing height of a bar or line on the plot



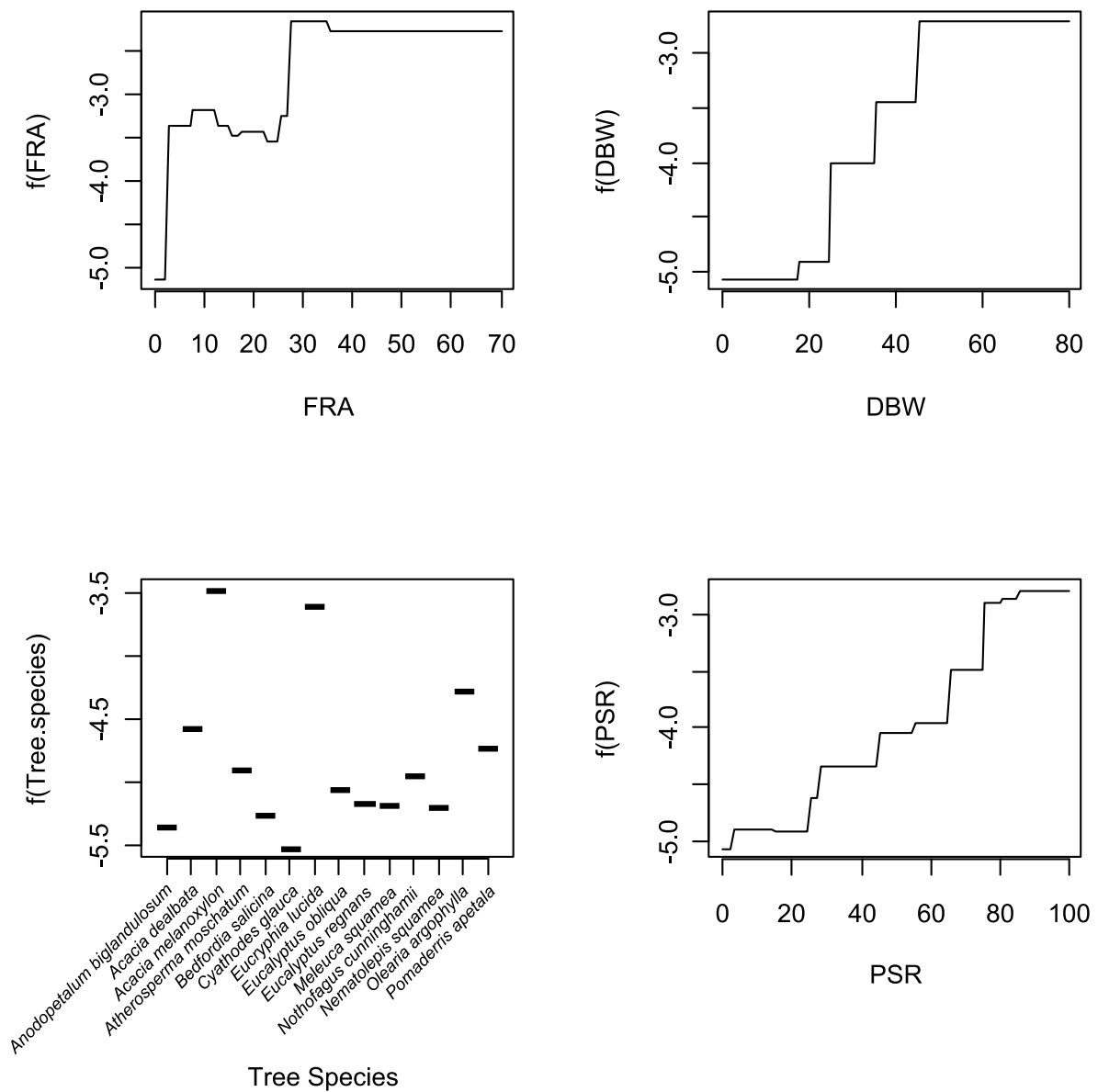
**Figure 5.10b** Functions fitted for the four most influential predictor variables in the boosted regression tree model (BRT) relating the probability of occurrence of *Prostomis atkinsoni* to its CWD environment. See Table 5.2 for rotten-wood types, Table 5.3 for CWD variables and Table 5.4 for an explanation of CWD-site variables. The probability of species occurrence increases with the increasing height of a bar or line on the plot.



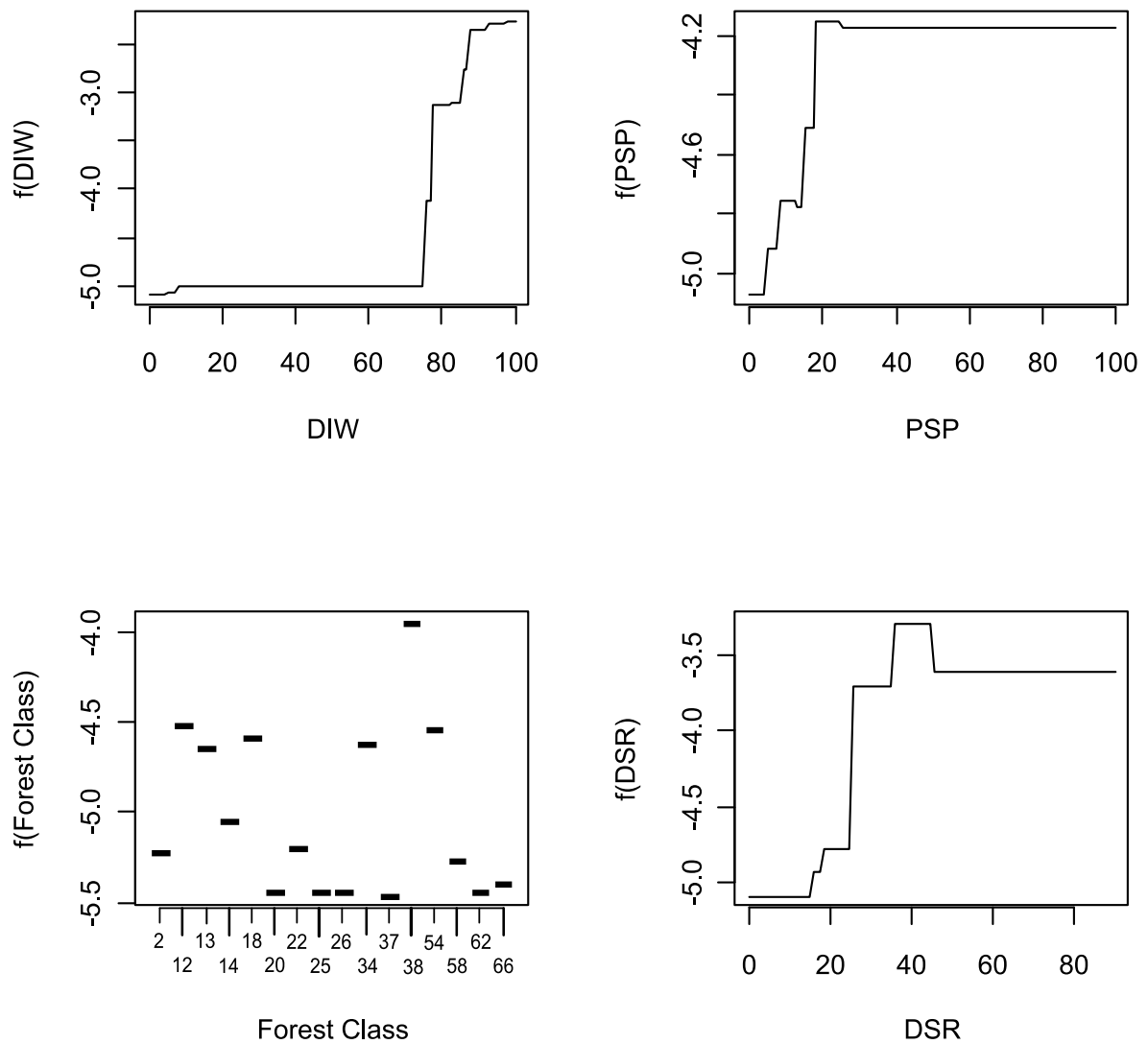
**Figure 5.11a** Functions fitted for the four most influential predictor variables in the boosted regression tree model (BRT) relating the probability of occurrence of *Dryophthorus* ECZ sp. 02 to its CWD environment. See Table 5.2 for rotten-wood types, Table 5.3 for CWD variables and Table 5.4 for an explanation of CWD-site variables. The probability of species occurrence increases with the increasing height of a bar or line on the plot.



**Figure 5.11b** Functions fitted for the four most influential predictor variables in the boosted regression tree model (BRT) relating the probability of occurrence of *Dryophthorus* ECZ sp. 02 to its CWD environment. See Table 5.2 for rotten-wood types, Table 5.3 for CWD variables and Table 5.4 for an explanation of CWD-site variables. Table 5.7 explains the habitat attributes of each forest class (see forest class plot, bottom left). The probability of species occurrence increases with the increasing height of a bar or line on the plot.



**Figure 5.12a Functions fitted for the four most influential predictor variables in the boosted regression tree model (BRT) relating the probability of occurrence of *Toxentes arcuatus* to its CWD environment. See Table 5.2 for rotten-wood types, Table 5.3 for CWD variables and Table 5.4 for an explanation of CWD-site variables. The probability of species occurrence increases with the increasing height of a bar or line on the plot.**



**Figure 5.12b** Functions fitted for the four most influential predictor variables in the boosted regression tree model (BRT) relating the probability of occurrence of *Toxeutes arcuatus* to its CWD environment. See Table 5.2 for rotten-wood types, Table 5.3 for CWD variables and Table 5.4 for an explanation of CWD-site variables. Table 5.7 explains the habitat attributes of each forest class (see forest class plot, bottom left). The probability of species occurrence increases with the increasing height of a bar or line on the plot.

## 5.4 Discussion

An exploratory technique and a modelling approach successfully identified the local CWD habitat requirements of six saproxylic beetles in wet-eucalypt production forests of Tasmania. Environmental data collected from CWD habitat produced habitat models which predicted presence/absence of the six beetles (within the study area), by distinguishing what CWD-scale predictor variables were most important in predicting presence/absence of each species. However, to confirm the predictive power and thus validate the model, field surveys should be conducted.

Some beetles had very specific CWD requirements while others were less selective. The sampling regime required to collect data that informed the models applied in this study is very time-consuming. Perhaps developing models using data from greater spatial scales available through GIS databases or forest inventories may be less intensive and equally successful at predicting beetle presence/absence.

### 5.4.1 Association between rotten-wood types and species presence/absence and relative abundance

Results showed that the presence and relative abundance of different saproxylic beetles is influenced by the local spectrum of rotten-wood types, in species-specific ways. Of the five species studied, two species (*P. atkinsoni* and *Dryophthorus* ECZ sp. 02) exhibited strong associations with a single (but different) rotten-wood type, while the remaining three species (*C. deplanata*, *L. menalcas* and *L. cancroides*) appeared to have much broader microhabitat preferences. These findings are consistent with those of Yee (2005), who found a positive association between beetle presence and rotten-wood types in *E. obliqua* logs.

The threatened stag beetle, *L. menalcas*, and its more widespread congener *L. cancroides*, largely exploited the same rotten-wood types, being strongly associated with the darker rotten-wood types (mudguts, dark brown fibrous and dark borer wood). However, *L. cancroides* was also found in rotten-wood types that are characteristic of early and very late decay stages (fibrous surface rot and humus-soil), and that have low moisture content (dark blocky crumbly rot). Species that are able to exploit a wide range of habitats are expected to become

both widespread and locally abundant (Lawton 1993; Brown 1984). Hence, the ability of *L. cancroides* to exploit a wider range of rotten-wood types than *L. menalcas* may explain its greater abundance in this habitat. In future, it would be interesting to assess the extent to which saproxylic beetles that are able to exploit several rotten-wood types exhibit wider ranges and/or greater abundance than those that are restricted to a narrower range of rotten-wood types.

*Predictive habitat models suggest that dark rotten-wood types facilitate species presence*

An interesting result of this study was that all of the study species were found exclusively in dark rotten-wood types. This is consistent with the findings of Yee (2005) who found that the greatest diversity of saproxylic beetles in this study area occurred in dark rotten-wood types. Indeed, Yee (2005) reported that only one saproxylic beetle, the cerambycid *Enneaphyllus aeneipennis*, was associated with a pale rotten-wood type. However, field observations from this study show that on rare occasions *L. cancroides*, *C. deplanata* and *T. arcuatus* can also be associated with pale rotten-wood types such as pale pocket rot (*PPR*), pale stringy rot (*PSR*) and pale spongy rot (*PSP*). The study species ‘prefer’ inhabiting dark rotten-wood types. The preference for dark rotten-wood types may be because they contain specific fungi or bacteria that the beetles can feed on, in which case the presence of such microorganisms might give rise to the beetles’ preferences. Mycophagy of saproxylic fungi with external sporocarps has been established in some groups of saproxylic beetles, with beetles selecting to feed on certain fungi (Jonsson and Nordlander 2006; Tanahashi *et al.* 2009) but the preference for fungi within rotten wood is largely unknown. Fungi inside the log do not necessarily produce external sporocarps. External sporocarps are often highly visible and therefore easy to sample and identify. For example, the polypore *Fomitopsis pinicola* is a large fungus that grows on the outside of decomposing logs and has been the focus of many studies (Jonsell and Nordlander 1995; Hågvar and Steen 2013; Pouska *et al.* 2013). Beetles located inside a log could be xylophagous or mycophagous but it is difficult to establish either when fungi and beetles occur within the decomposing log and cannot be seen with the naked eye. Using current molecular tools may help establish if certain fungi determine rotten-wood type and presence of saproxylic beetles (Chapter 4).



*Moisture can influence species presence/absence*

The results of this study revealed that other features of dead wood aside from rotten-wood type can also influence species presence/absence. For example, *Dryophthorus* ECZ sp. 02 was most closely associated with wet cracks. These fractures in the dead wood hold water and appear to provide a moist habitat for this species. Previous studies have shown that the moisture content of dead wood increases the abundance of insects that can be found (Schiegg 2002). Another feature strongly associated with the presence of particular species(e.g. *L. menalcas*) was the frass of the wood-boring cerambycid, *T. arcuatus*. This association is likely to be ecologically significant, as beetles feeding on the frass of other insects are thought to be obtaining fungi to aid in the digestion of rotting wood (Chapter 4).

*Resource partitioning may explain lack of species co-occurrence in rotten wood*

The results of this study suggest that there is resource partitioning occurring in this group of species. There was some overlap between species and rotten-wood types but in general most species shared rotten-wood types; however, the study species did not co-occur on a rotten-wood type within the sampled part of the log. Resource partitioning is a mechanism that can facilitate persistence among individuals competing for access to scarce or transient resources (Errouissi *et al.* 2004). However, as the study species appeared to inhabit different rotten-wood types then it could be argued that competition for resources may be low (though more competition would be expected for those species restricted to a narrow range of rotten-wood types). A complex mix of environmental and physical factors can influence the life-span and decay process of a decomposing log, making it difficult to ascertain whether this beetle group employs resource partitioning. To date, resource partitioning has not been used successfully to explain beetle assemblages in dead wood. As our understanding of dead wood dynamics improves (a research area that has received recent attention in Tasmania; Grove *et al.* 2009; Grove and Stamm 2011; Grove *et al.* 2011) it will be possible to investigate how saproxylic beetles live within a log as it goes through successive stages of decomposition. This knowledge together with an understanding of which rotten-wood types are associated with particular decay stages will allow us to explicitly address the reason that saproxylic beetles do not seem to co-occur.

*The influence of CWD attributes and CWD-site characteristics on beetle presence*

The results of this study demonstrate that CWD rotten-wood type is the primary determinant of the presence of saproxylic beetles. The addition of CWD-site characteristics that influence CWD attributes (e.g. log length, fire frequency, age of forest regeneration and tree species) to predictive habitat models did not improve the predictive ability of models. Hence, the results of predictive habitat modelling support those of the previous correspondence analysis, showing a subdivision of habitat among the study species with specific, and often unique, associations with different rotten-wood types. Indeed the presence or absence of all species could be predicted with a very high probability solely by knowing the type (or types) of rotten wood that comprised a piece of CWD; however, some of the models included CWD-site characteristics such as *forest class* and *age of regen* indicating these variables were also useful in predicting presence/absence. Being able to adequately predict species presence/absence of the beetles using CWD-site scale variables may offer an easier solution for future management, because these predictor variables, being sourced from GIS databases, require less effort to obtain data from than sampling CWD for different types of rotten wood.

Many saproxylic beetles share an intimate relationship with wood-decay fungi and the rotten-wood types that are formed by them (Gilbertson 1984). Recent studies in Tasmania by Yee *et al.* (2001) and Hopkins (2007) have provided a detailed classification of many rotten-wood types and fungal isolates and, thus, provide a foundation for understanding this complex relationship. For instance, Yee *et al.* (2001) isolated over 700 basidiomycete fungal species from just eight rotten-wood types. Similarly, in Chapter 4 of this thesis over 20 morphotypes of wood-decay fungi were identified from a single rotten-wood type. This knowledge can help to understand the nature of associations between saproxylic beetles and rotten-wood types, and ultimately, contribute to the effective management of wet-eucalypt habitat at the CWD level (See Chapter 4).

A key result of this study was that dark rotten-wood types appear to be a major habitat requirement for all of the species studied. Ecological processes which produce dark rotten-wood types are important for maintaining the presence of these beetles in the environment and conserving these species should involve management activities that allow those ecological processes to persist. Results showed that gingerbread type rot (*GBR*) is ecologically very important for *P.*

*atkinsoni*, as this species was found almost exclusively in this rotten-wood type and may in fact engineer it (Yee 2005). Likewise, *Dryophthorus* ECZ sp. 02 was found almost exclusively in mudgut rot (*MUD*) and dark brown fibrous rot (*DBF*), while the threatened stag beetle *L. menalcas* and its non-threatened relative *L. cancroides* were associated with mudgut rot (*MUD*) and dark borer wood (*DBW*). In accordance with this finding model results also showed strong associations between the presence of the six study species and intermediate decay stages, when the diversity of rotten-wood types and particularly dark rotten wood was highest. Unsurprisingly, few beetles in this study were present in CWD that was in late decay (i.e. when the log was practically a part of the forest floor), or in the early stage of decay (when logs contained few rotten-wood types), though other studies have indicated that as CWD decays it is colonised by a diverse succession of saproxylic insect species (Hammond *et al.* 2001; Grove 2002). Although the preference for intermediate decay stages by this guild of saproxylic beetles is an intuitive result, it has not previously been demonstrated. However, similar associations between saproxylic beetles and dark rotten-wood types have been reported from studies conducted in similar forest types in Tasmania and Japan (Araya 1993; Yee *et al.* 2004; Yee 2005). This intimate relationship between saproxylic beetles and dark rotten-wood types suggests that these species may decline if dark rotten-wood types decline. Although there is no evidence to suggest that dark rotten-wood types are more vulnerable than pale rotten-wood types, dark rotten wood is associated with old and large-diameter eucalypt CWD (Wardlaw *et al.* 2009 and Grove *et al.* 2011), which is vulnerable to depletion by frequent timber harvesting (harvesting on short rotation) and by frequent wildfires.

*Tree species can determine the presence of some study species*

Model results revealed that the species of tree from which CWD is derived can be an important habitat characteristic for predicting the presence of saproxylic beetles. All six species studied were located more often in eucalypt CWD than in CWD derived from other tree species, with at least one of the beetles, *Dryophthorus* ECZ sp. 02, found exclusively in eucalypt CWD. It is perhaps unsurprising that many saproxylic beetles have adapted to living in the CWD of eucalypts, as eucalypts dominate wet sclerophyll forests. Nevertheless, some species preferred CWD from tree species other than eucalypts. For example, *L.*

*menalcas* presence was associated with CWD derived from *Acacia melanoxylon*, while the presence of *T. arcuatus* was associated with CWD derived from *A. dealbata*. The preferences of these species for CWD from tree species other than *E. obliqua* and *E. regnans* has not been previously documented for this group of Australian saproxylic beetles. These associations are unlikely to be explained by difference in the type of rotten wood formed from eucalypt and non-eucalypt tree species as there is no data to suggest that such differences exist. However, wood inhabiting fungi specific to particular trees is known to influence the presence of saproxylic beetles elsewhere (Økland *et al.* 1996). Moreover, other studies have found that saproxylic beetles show preferences for particular host trees, though this most commonly occurs at the genus, rather than the species, level (Tavakilian *et al.* 1997; Köhler 2000). It is important to note however, that patterns of associations between saproxylic beetles and dead wood is likely to differ in Australia compared to those seen in Europe and other parts of the world, because so many Australian forests are dominated by a single tree genus, *Eucalyptus*.

In addition to tree species, model results showed that the presence of saproxylic beetles was significantly influenced (both positively and negatively) by forest regeneration age, as this can influence the dynamics and characteristics of CWD by creating more or less CWD with the preferred rotten-wood types. Interestingly, the results showed that young regenerating forest (particularly from 1996) was important for *P. atkinsoni*, *C. deplanata* and *Dryophthorus* ECZ sp. 02, and *L. menalcas*. As young trees (and hence young CWD) are too young to contain the types of rotten wood that these species require, these results suggest that these species were able to survive in these forests by utilising legacy CWD (CWD remaining from forest that existed prior to the CBS harvesting activity in 1996). The amount of wood left on the ground following harvesting varies according to the type of forest, the history of the stand, the enthusiasm of the contractor and the assiduousness of the supervisor in checking the coupe pulpwood markets (Mark Neyland, pers. comm.). During the 1990s the volume of CWD left on the forest floor may have been high due to different methods of tree harvesting reflecting consumer need. For instance, in the past there have been fluctuations in the pulpwood markets that have had a major impact on post-logging residue levels (Tim Wardlaw, pers. comm.). Alternatively, however, beetles may have been able to colonise the CWD by migrating from surrounding forest. Lindenmayer *et al.*

(2006) proposed that retaining mature standing trees as pre-existing habitat which can act as a ‘lifeboat’, to provide habitat features that are not recruited within typical logging rotations. The findings reported here support the ‘legacy CWD’ proposal and emphasise the need for substantial volumes of CWD from older forest stands to be left on the ground after forest harvest. Pre-existing CWD may also promote a more heterogeneous CWD environment, a feature much needed for the persistence of saproxylic beetles (Michaels and Bornemissza 1999; Grove 2002).

The results of the BGLM indicated that *C. deplanata* and *Dryophthorus* ECZ sp. 02 preferred regenerating forest from 1982 and 1983. These latter forests are perhaps structurally more diverse and have possibly produced CWD at varying decay stages and therefore may support logs with rotten-wood type habitat suitable for the study beetles. Field observations imply that coarse woody debris produced since the 1986 harvesting of the site would support rotten-wood types that are now beginning to be exploited by some of the study species. Overall, the preferences shown by different beetles for areas of forests with particular regeneration ages suggests that the structural attributes of a forest can affect the diversity and abundance of its beetle fauna.

*The influence of forest class on the presence of saproxylic beetles*

The forest class variable in both models often contradicts with the age of regenerating forest (*age of regen* variable). For example, the model for *C. deplanata* chooses *forest class 54* as a predictor of presence for this species. *Forest class 54* describes a forest that is regenerating from 1967 and 1979. The description of forest from *forest class 54* is markedly different from 1996 regenerating forest. The reasons for this are biologically unclear but may have something to do with overfitting of the model or the ‘lifeboat’ hypothesis mentioned earlier in this section. For these reasons it was decided that the model be rerun with age of regeneration from the 1990s and forest class taken out. Doing this however, made no difference to the performance or interpretation of the model and in some cases the model performance was decreased.

Because the forest class system is very site specific and contains many different forest attributes it is difficult to find a broad way of utilising this system in the model; however, in Section 5.2.3, Table 5.7 and 5.8 describe the information from

the *forest class* and *broad forest class* predictor variables which has helped to solve this issue. Initially a ‘broad forest class’ was used, which placed the forest classes into their respective groups (Table 5.7) but the performance of the model was greatly decreased suggesting that forest attributes identifying species presence were lost when aggregating the forest classes. So models that contain the forest class predictor variable will need to be interpreted using Table 5.7 to make some generalisations about habitat requirements of the species at the CWD-site, if they are to be used as a planning tool. However, the forest industry may choose to incorporate generalisations arising from the exploration of models into the planning process, treating the species as a group rather than individually.

#### 5.4.2 Limitations and caveats

One shortcoming of the approach adopted in this study to determine microhabitat preferences of saproxylic beetles is that recorded absences of species do not necessarily imply that a particular microhabitat is unsuitable for that species, nor, indeed, that the species was truly absent. Rather, absences are likely to be a consequence of the fact that sampling was not exhaustive. Alternatively, absences could also occur if the local distribution of these species is influenced by temporarily unsuitable conditions combined with an inability to disperse to suitable habitat due to fragmentation of this habitat. An assessment of the influence of stochastic environmental variation on the spatial distribution of saproxylic beetles requires detailed knowledge of the natural history of the study species (Matern *et al.* 2007). This information is currently limited for most species (see Chapter 3 and 4). Nevertheless, future studies to elucidate the dispersal capabilities and dynamics of these species should provide a more robust understanding of their ability to persist in fragmented landscapes.

A further shortcoming of this study is that the classification of rotten-wood types is resolved to an extremely fine scale (i.e. many categories of rotten-wood needed to be included in predictive models). Multiple rotten-wood types are commonly found intermingled in a single piece of dead wood (Yee 2005; Grove *et al.* 2011), and this network of different rotten-wood types leads to complicated multivariate models. Although this approach was necessary in this study due to the lack of knowledge of the succession of rotten-wood types, model results may be too complex to be of practical use (e.g. for devising management strategies).

Habitat predictor variables such as *most recent fire*, *age of regen* or *forest class* differed marginally between species, with most species sharing the same key attributes of these variables. However, specific habitat variables were identified for most species, but their performance in most instances did not outweigh the rotten-wood type predictor variables. This suggests one of two things: firstly, when modelling for species presence/absence, rotten-wood types are the key predictor variables and simply outweigh other predictor variables or, secondly, these variables are not individually good at predicting presence/absence of the study species. Chapter 6 explores habitat modelling of the study species at the site- and landscape-scale where these latter predictor variables may be more influential because rotten-wood type and some CWD-site variables are omitted from the model at these greater spatial scales.

#### **5.4.3 Habitat specificity present a challenge for managing saproxylic beetles**

The results of this chapter reveal that saproxylic species have complex and species-specific microhabitat preferences that lead to divergent exploitation patterns among species in how they utilise CWD habitat. To date, our knowledge of these species' ecological preferences has been extremely fragmented and largely limited to their general association with CWD of *Eucalyptus obliqua* logs (Yee 2005) and their restricted distribution throughout the wet-eucalypt forests of southern Tasmania (Meggs and Taylor 1999). This study, thus, greatly extends knowledge of the fine-scale habitat preferences of this group of saproxylic beetles in southern Tasmania, revealing their preferences for particular rotten-wood types, certain tree species and logs of at an intermediate stage of decay. Accordingly, this work has highlighted the importance of the maintenance of tree species that contain dark rotten-wood types and old trees in the continual replenishment of CWD.

That the majority of the study species exhibited a degree of specificity in their habitat preferences presents a challenge for conserving these species as a group. However, their shared, broader preferences for rotten-wood types and mid-decay stage logs, implies that most will have some of their habitat needs catered for under current silviculture regimes. To further improve silviculture practices so as to better manage CWD resource for saproxylic beetles an understanding of variation in this resource both spatially and temporally is needed. Modelling

CWD quality and quantity changes over time has been made possible with the research by Stamm (2006) and Grove and Stamm (2011), and understanding of CWD decomposition by Grove *et al.* (2009 and 2011). For instance, the ecology of decomposition in Tasmania's wet-eucalypt forest is adequately captured by a decay classification system (Grove *et al.* 2011). Combining the predictive habitat models from this study with the CWD modelling of these authors may reveal synergistic dynamics that are important both for promoting the continuity of these habitats in the landscape, and for ensuring the continued persistence of saproxylic beetles.

This study has identified the some fine-scale habitat preferences of six saproxylic beetles for CWD resources in wet sclerophyll forest. As advocated by Yee *et al.* (2001), this understanding is a prerequisite for developing meaningful indicators that will assist in the monitoring and management of CWD-dependent beetles in wet-eucalypt production forests.



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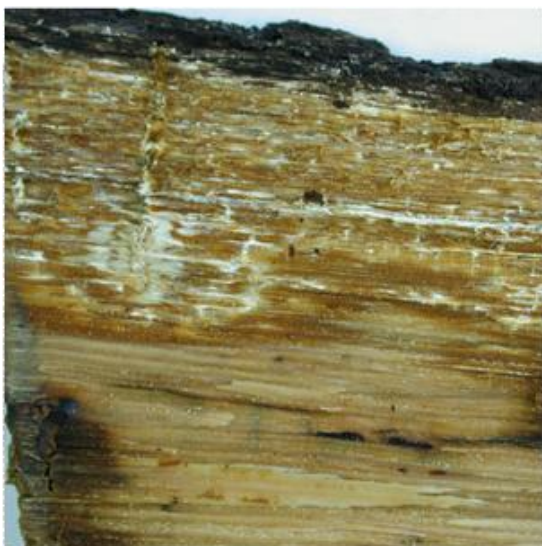
## APPENDIX 5.1 ROTTEN-WOOD TYPES

All descriptions, unless stated otherwise, are taken with permission from Hopkins (2007).



### **Discoloured wood - DIW**

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.



### **Fibrous surface rot - FSR**

Fibrous surface rot occurs in the top 1 – 5 cm of the log surface layer but can extend into the outer heartwood. It has a soft stringy texture, ranging from grey-white to straw or brown. Fibrous surface rot appears to consist of numerous minute irregular pockets, speckled with soft bleached fibres.

**Dark blocky crumbly rot - DBC**

Dark blocky crumbly rot is characterised by brittle wood that breaks off in regular blocks and can be crumbled to powder by hand. It is tan or light brown in colour and consistently contains very dry sheets of mycelium, with a chamois-like texture that progress along the rays.

**Dark stringy rot - DSR**

Dark stringy rot has a coarse stringy texture, ranging from light brown through to dark reddish-brown. It appears to consist of long, stringy, wool-like fibres.

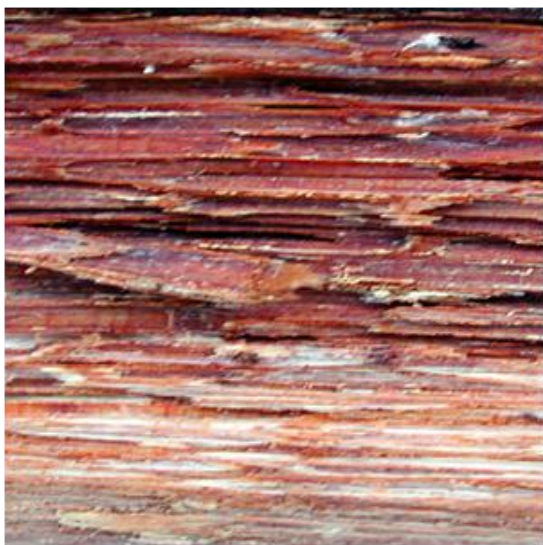


**Dark blocky fibrous rot - DBF**

Dark blocky fibrous rot is a distinctive red-brown in colour and commonly breaks into irregular blocks that maintain a soft, fibrous texture. Even when the wood is hard, the fibres can be teased apart, though, in more decomposed wood, the fibres are moist and soft, giving a spongy texture.

**Dark borer wood - DBW**

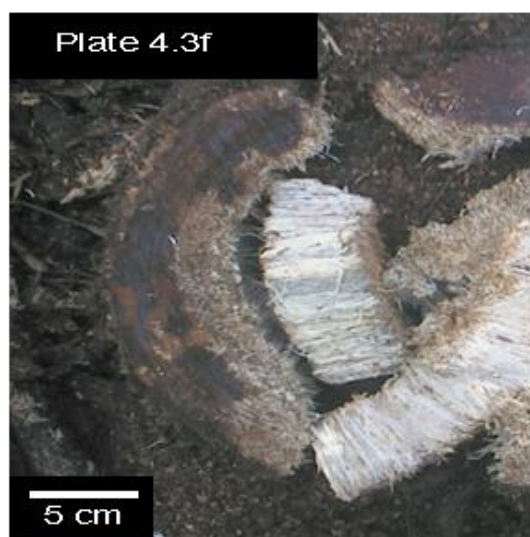
Dark borer wood consists of a fibrous or spongy red-brown rot, which is rather moist and contains galleries of termites or other borers.

**Pale pocket rot - PPR**

Pale pocket rot is characterised by 5 – 20 mm regular round to elliptical pockets, which are either empty or are filled with white gelatinous material (cellulose), or may be lined with white or yellow mycelium. These pockets are separated by thin areas of seemingly intact wood.

**Pale spongy rot - PSP**

Pale spongy rot is characterised by continuous long, spongy, wool-like, bleached fibres that can range in colour from white to a straw-yellow. It has a very soft texture and appears to have a very low density.



### **Pale stringy rot - PSR**

Pale stringy rot is composed of continuous long, spongy, wool-like, bleached-white fibres, adjacent to which lies solid wood that is crimson to dark brown in colour. This rotten-wood type is often associated with the outer heartwood, and is sometimes in contact with the log surface, though columns occur within the inner heartwood.



### **Mudguts - MUD**

Mudguts has a characteristic clay-like consistency, and appears devoid of recognisable wood fibres. Mudguts mostly occurs in the inner heartwood, sometimes associated with a hollow, but also occurs in localised patches in the outer heartwood, and often adjacent to red-brown blocky fibrous rot.





### **Jelly surface rot - JSR**

Jelly surface rot is characterised by large (> 50 mm) irregular pockets which may be empty or filled with white, soft, very wet, gelatinous material. These pockets are demarcated by black 'zone' lines. Rhizomorphs also present in these pockets.



### **Gingerbread rot - GBR**

Gingerbread rot is characterised by its flattened smooth undulating dark brown surface, similar in appearance to gingerbread. It has a consistency not unlike putty and is quite moist.



### **Charcoal - CHA**

Charcoal arises via wildfire or lightning strikes and can occur embedded in other rots or as rubble where a former log lay or where a former tree stood.

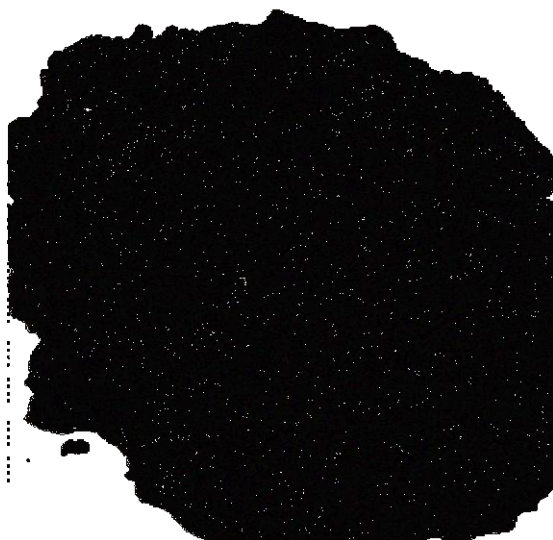


### **Frass - FRA**

Frass is a rotten-wood type comprised of accumulations of the droppings of arthropods such as wood-boring beetles and termites and was originally thought to be dark borer wood (DBW; Hopkins 2007). Substantial deposits of frass can form at the base of hollows. In this study frass refers to frass that has formed exclusively from the droppings of *T. arcuatus*.

### **Humus - HUM - not illustrated**

Humus constitutes the dark brown to black organic material found in well-decayed logs. When rubbed between the forefinger and thumb it crumbles into small particles.



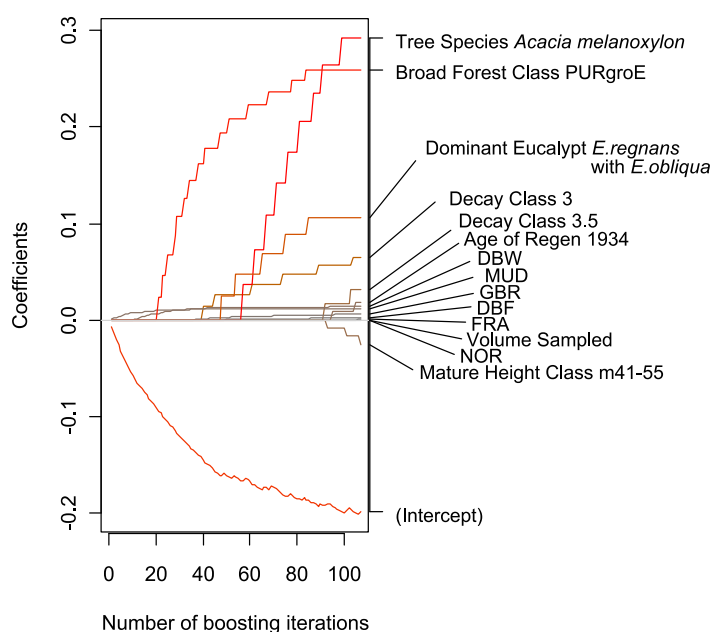
### **Humus soil - HSO**

Humus soil is a soil-like substance that smears with a silt-like texture when rubbed between the forefinger and thumb. It is dark brown to black in colour and common in the inner heartwood area.

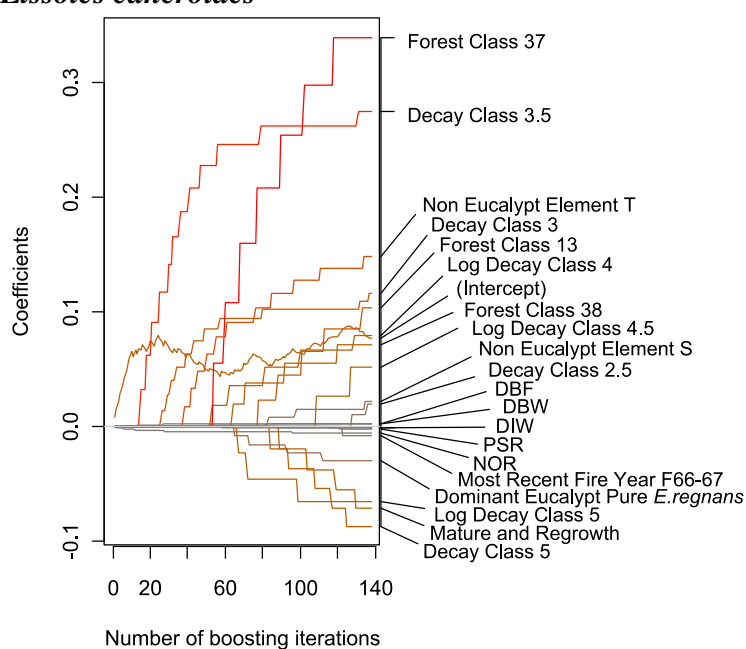
## APPENDIX 5.2 BOOSTED GENERALISED LINEAR MODELLING PLOTS WITH CWD-SCALE PREDICTOR VARIABLES

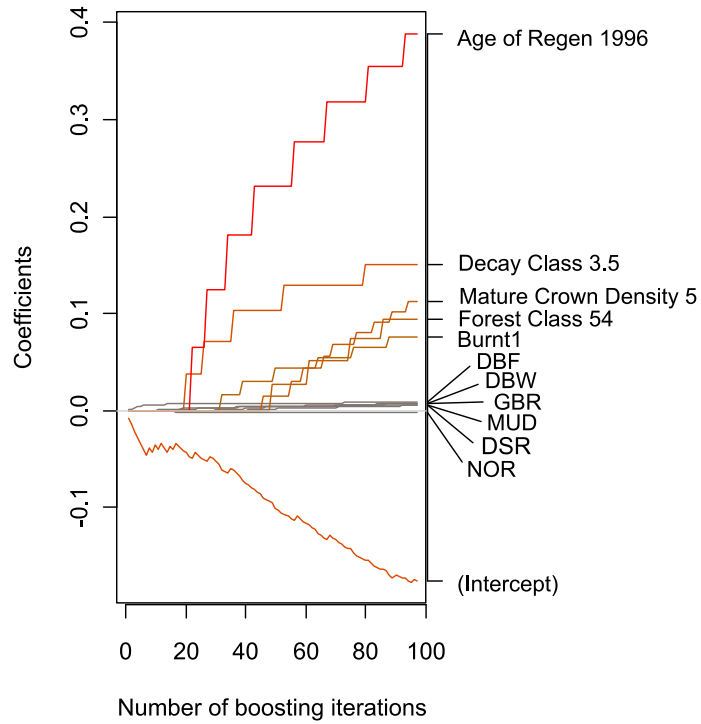
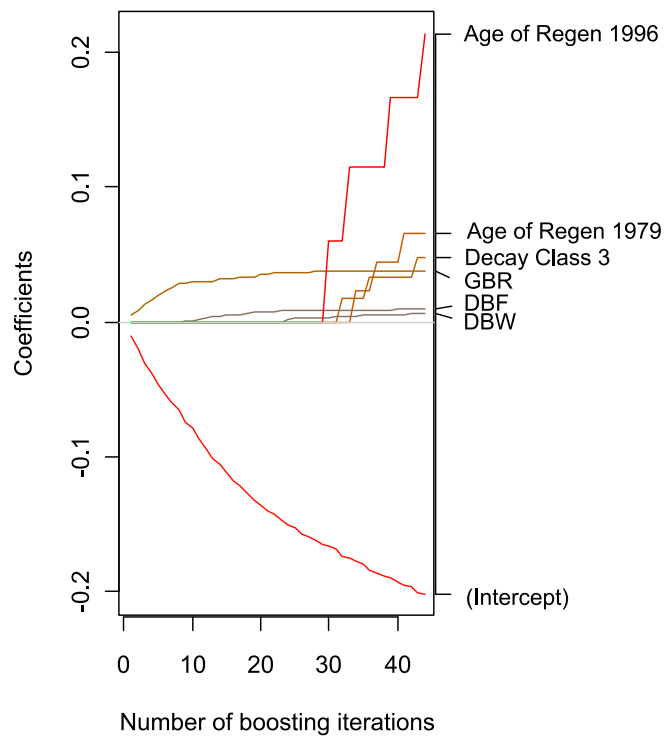
Those variables most influential in predicting the presence/absence of this species are introduced into the model early in the boosting iterations. For example for the *L. menalcas* plot below tree species *A. melanoxylon* is introduced after 20 iterations whereas decay class 3.5, a less influential variable, is introduced after 80 iterations. Those variables with a negative coefficient are predicting absence.

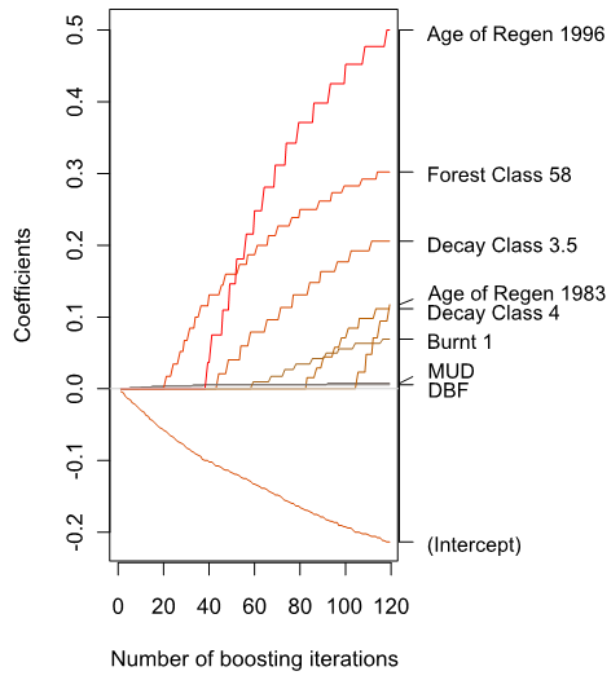
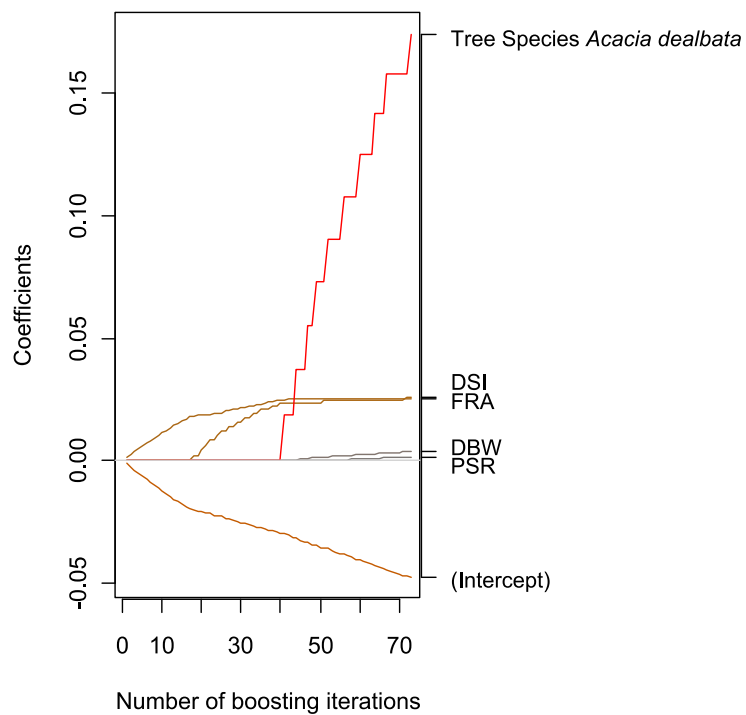
### *Lissotes menalcas*



### *Lissotes cancroides*



*Coripera deplanata**Prostomis atkinsoni*

***Dryophthorus* ECZ sp. 02*****Toxeutes arcuatus***



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## CHAPTER 6 CAN SPECIFIC ATTRIBUTES AT THE SITE- AND LANDSCAPE-SCALE, EITHER SINGLY OR IN COMBINATION, DETERMINE THE PRESENCE OF SIX SAPROXYLIC BEETLES IN WET-EUCALYPT PRODUCTION FORESTS OF SOUTHERN TASMANIA?

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### 6.1 Introduction

Habitat selection is a major determinant of species distribution (Guisan and Thuiller 2005) and is important to understand when predicting how a species will respond to natural or anthropogenic alteration of its habitat (Ewers and Didham 2005). One such alteration is timber-harvesting and understanding the ecological consequences of timber harvesting on forest-dependent species is important for managing forests in a sustainable manner and for protecting forests-dependent species. The use of ecological modelling techniques can help examine habitat-specific responses of organisms. Such techniques have allowed researchers to identify the current and potential distributions of species, predict the extent and location of suitable habitat, and understand the consequences of environmental perturbation for species persistence. For example, Mateo-Tomás and Olea (2010) used models to determine the ecological factors that shape the current and potential breeding distribution of threatened griffon vultures in north-western Spain. Their model showed that griffon vultures could potentially increase their present breeding range, but that mitigation will be needed to manage proposed wind farm developments that will cover 7.22% of this potentially suitable habitat (Mateo-Tomás and Olea, 2010). However, as in this example, most studies modelling species distributions over large landscape-scales have focused on understanding the distributions of iconic vertebrates (e.g. wolves, Corsi *et al.* 1999). In contrast, such models have not been extensively applied to invertebrates, and rarely to beetles (Meggs *et al.* 2004; Diniz-Filho *et al.* 2010). The purpose of this chapter is to develop models that attempt to characterise the habitat preferences of six saproxylic beetles (those that are dependent on dead wood at some stage in their life cycle) (*Lissotes menalcas*, *Lissotes cancroides*, *Prostomis atkinsoni*, *Coripera deplanata*, *Dryophthorus* ECZ sp 02 and *Toxeutes arcuatus*)

by using predictive habitat models to identify their preferred habitat at the site- and landscape-scale.

The modelling described in this chapter focuses on the current distribution patterns of six saproxylic beetles in a production-forest matrix and aims to (i) identify their specific habitat requirements and (ii) determine whether site- and landscape-scale environmental variables can predict the presence and distribution of these species. When coupled with landscape simulations this work can reveal how a species responds to alternative forest management scenarios (Vernier *et al.* 2008), which is an important step for understanding saproxylic beetle persistence in altered landscapes (e.g. a production-forest matrix). For example, a hierarchical decision-support system (which includes a stand-level model, a forest estate model, a habitat model and a visualization model) has been used in British Columbia to evaluate multi-objective management options for a 288,000 ha forest (Seely *et al.* 2004).

Identifying suitable habitat for vulnerable and threatened saproxylic beetles is necessary to develop and implement adequate conservation strategies (Siitonen and Saaristo 2000; Thomaes *et al.* 2008; Götmark *et al.* 2011). Grove (2006) suggests that identifying suitable habitat is a good strategy for managing saproxylic beetles when there is a thorough ecological understanding of the species in question. Intensive surveying undertaken to establish ecological requirements is often necessary, but can be time-consuming and not always cost-effective. Remotely obtained environmental information from geographic information systems (GIS) and remote sensing coupled with photographic interpretation, is considered an important, cost-effective, and preferred method of constructing predictive habitat models in comparison to on-ground surveys (Kushwaha and Roy 2002). For this reason, an additional aim of this chapter was to establish whether site- and landscape-scale variables (indicative of environment features on a scale from tens of metres to several kilometres) could robustly predict the presence/absence and distribution of saproxylic beetles in the environment, and thus alleviate the necessity to conduct intensive, on-ground surveys to characterise fine-scale habitat features (e.g. rotten-wood types, Chapter 5). The following subsections introduce habitat attributes thought to be useful for predicting the presence of saproxylic beetles at large spatial scales.

### 6.1.1. Variables likely to influence the presence and distribution of saproxylic beetles at the site- and landscape-scale

#### *Volume of coarse woody debris (CWD)*

Volume of CWD has been shown to be correlated with the diversity and abundance of saproxylic beetles in many parts of Europe (Grove 2002), and is also the best predictor of species richness of beetles in Queensland's lowland tropical rainforest (Grove 2002a). In addition, the absence of larger-diameter trees from logged forest in Queensland's lowland tropical rainforest was correlated with observed differences in the abundance and composition of the saproxylic beetle fauna assemblage (Grove 2002a). Similarly, a significant correlation between CWD volume and the species richness of saproxylic beetles was related to several predictors at the forest stand level in a European study (Lassauce *et al.* 2011). Unsurprisingly, therefore, increasing the volume of CWD is a suggested strategy for managing saproxylic beetles in many European countries. Tasmanian wet-eucalypt forests differ to European forests as they contain large amounts of CWD (Woldendorp *et al.* 2002; Humphrey *et al.* 2004). Nevertheless, volumes of CWD may still vary over time as a result of differences in tree species, site productivity, fire history and management practices. Consequently, Tasmanian saproxylic beetle species might be expected to respond differently from their European counterparts to the availability of CWD apparent across large spatial scales.

#### *Stand structure*

Stand structure is a term used to describe characteristics of a forest stand and it is dictated by processes and activities the forest stand has been subjected to. For the purposes of this study variables such as time since last fire and age of regenerating forest determine the structure of a forest stand (see methods section for more detail on variables that influence stand structure). Stand structure is a useful predictor of species presence (Hynynen *et al.* 2005; McGeoch *et al.* 2007; Müller *et al.* 2008) and this extends to saproxylic beetles (Grove 2002a; Micó *et al.* 2013; Norvez *et al.* 2013). For example, Müller *et al.* (2008) showed that in deciduous beech forest any form of logging will reduce the numbers of species in several taxa (birds, saproxylic beetles and wood inhabiting fungi) because they have higher demands for structures typical of pristine forests (forests with no timber harvesting for greater than 25 years). These relationships probably arise because of the correlation between stand structure and standing biomass that indirectly

links it to the amount of future CWD (i.e. stand structure may be a surrogate for future volumes of CWD). Økland *et al.* 1996 found that diversity in different groups of obligate saproxylic beetles was related to environmental variables, including vegetation structure, at three spatial scales in mature spruce-dominated forest. This suggests that vegetation structure may be an important factor to consider when measuring the diversity of saproxylic beetles.

The majority of studies ignore the spatial and temporal variability of stand structure. To use stand structure effectively as a predictor of saproxylic species presence, processes that create dead-wood substrate must be understood. Disturbance, both natural and anthropogenic influence the age and structure of forests and, consequently, the resulting CWD habitat. In this study, these elements of the stand structure will be incorporated into analyses in the form of different categories of forest classes (see Chapter 5, Section 5.2.3 for an explanation of the forest class system).

#### *Aspect and geology*

Geology and aspect are biophysical features that can determine soil fertility, influence productivity, and thus act as proxies for other processes that influence the creation of CWD. For instance, sites in the study area with southern aspects have lower insolation and higher moisture levels than north-facing slopes (Kirkpatrick and Nunez 1980). The high moisture coupled with higher productivity (in terms of forest biomass) leads to less frequent fires but when they do burn there is a lot of fuel on the ground to sustain them (Harris and Kitchener 2005) so they may be able to introduce CWD to the forest floor.

Although few studies have focused on aspect and geology as major predictors of forest insects across landscapes, these variables have been shown to influence large-scale modelling of species distributions and abundance (Thomaes *et al.* 2008; Murray *et al.* 2009). It is possible, therefore, that the aspect and geology of a site exerts as stronger an influence on the presence of saproxylic beetles as do environmental variables operating at smaller spatial scales (i.e. at the CWD-scale, see Chapter 5). However, studies examining the influence of these variables on the distribution of saproxylic beetles are rare. One study, by Thomaes *et al.* (2008), found that the threatened saproxylic stag beetle *Lucanus cervus* is found more commonly on south-facing slopes. Thomaes *et al.* (2008) did not discuss the

reasons why the species was more common on south-facing slopes but it may be due to temperature related thresholds (Orrock *et al.* 2000).

#### *Historical factors*

Historical factors, such as historical glaciation patterns or geographical barriers to species dispersal, may influence regional patterns of faunal composition. For example, Tyler's Line in Tasmania is a region of transition in climate, geology, soil composition and vegetation, which runs north to south through the centre of the island, aslant the 146<sup>th</sup> meridian (Tyler 1992; Schultz *et al.* 2010). The ranges of many invertebrate taxa are exclusively either to the east or west of this line (Mesibov 1994). Similarly, Plomley's Island, a faunal break in the north-east of Tasmania, displays localised endemism of invertebrate taxa (Mesibov 1994, 1998). It is likely that these historical features may also influence the distribution of saproxylic beetles in Tasmania. For example, *Lissotes menalcas* has a restricted distribution (being confined to areas in the southeast and Bruny Island) for reasons which currently have not been identified. It is possible that rivers in this area prevent the dispersal of this species beyond its current range.

#### *Habitat modelling and environmental change*

Models that predict current suitable habitat in a given area may be useful in the future, in particular, when predicting how a species distribution might be affected by environmental changes. These current habitat models can be used to test the reliability of predicted future projections of distribution patterns under various climate change scenarios (Diniz-Filho *et al.* 2010). The number of studies modelling the effects of climate change on species distributions has increased in the past decade (Guisan and Hofer 2003; Aragón *et al.* 2010). Many of these models indicate that climate change is altering habitat and consequently species distribution (Lawler *et al.* 2006). In addition, these models have highlighted an increased risk of species extinction (Thomas *et al.* 2004), but in parallel a review by Diniz-Filho *et al.* (2010) examined studies that identified frontier habitat that has become suitable as a consequence of climate change, suggesting that risk of extinction is decreased if suitable habitat is increased by climate change.

In terms of climate change in Tasmania, current modelling suggests fewer impacts compared to mainland Australia (Climate Futures Tasmania website). Climate Futures Tasmania (CFT) states:

*“There will be some small changes in temperature but these are less than the projected global average temperature rise, due to the moderating influence of the Southern Ocean. The increasing temperature may lead to an increase in evaporation, decreased average cloud cover, increases in relative humidity and increased winds in spring. In addition to this, there has been a reduction in total annual rainfall in Tasmania since 1975. This reduction has been greatest in autumn, and is similar to other regions of southern Australia.”*

The changes in temperature and rainfall are suggestive of a ‘drier’ future climate. This warmer, drier weather is likely to change the current fire regimes observed in the study area, due to an increase in fire promoting weather (e.g. from 300 years to once every 100 years). What this means is a potential shift towards lesser amounts of mixed forest and wet-eucalypt forest. The likely impacts on CWD inputs include a reduction in volume of dead wood and altered decay rates and decay stages. These changes in CWD are likely to have a negative impact on the abundance of the study species by decreasing CWD habitat and the quality of this habitat at the forest stand and CWD level (direct impact on the CWD habitat).

### **6.1.2 Hypothesis and aims**

Developing predictive habitat models using site- and landscape-scale data alleviates the necessity to conduct intensive, on-ground surveys to characterise fine-scale habitat features (cf. rotten-wood types, Chapter 5). Consequently models at greater spatial scales are preferred by forest managers. In this chapter I attempt to establish the performance of predictive habitat models by testing the hypothesis that there are specific attributes of the physical environment at the site- and landscape-scale that, either singly or in combination, allow predictions to be made as to where six saproxylic beetles might be expected to occur. To test this hypothesis predictive habitat models for site-scale (boosted regression trees and boosted generalised linear models) and landscape-scale (generalised additive models) were developed. In order to substantiate this hypothesis and explain the presence/absence of the study species the following aims were established: (1) describe the specific site and landscape habitat requirements of six saproxylic beetles within wet-eucalypt production forest in Tasmania, using data collected from GIS database and forest inventories (2) using selected modelling techniques determine whether site- and landscape-scale environmental variables can predict

the presence/absence of these species in the allocated study area. The possible contribution of the predictive habitat models to the management of saproxylic beetles is then discussed using Tasmania's threatened stag beetle, *Lissotes menalcas* as an example.

## 6.2 Methods

### 6.2.1 Environmental variables

The presence or absence of the study species was the dependent variable used in this study and detail on how these data were collected is explained in Chapter 5. Twelve environmental variables were used (Table 6.1) to identify habitat requirements and predict species presence:

- Five environmental variables in the generalised additive models (GAM) to identify habitat requirements and predict presence at a landscape-scale of approximately 13 x 30 km: *distance to nearest river*, *geology*, *most recent fire*, *forest stage* and *aspect*
- Eleven environmental variables used in the boosted regression trees (BRT) and boosted generalised linear models (BGLM) at the site-scale of 100 x 100 m: *volume of CWD*, forest regenerating from silviculture or natural disturbance (*Rgr*, *Rgen* or *Mat/Rgr*), *most recent fire*, *age of regeneration*, *broad forest class*, *forest class*, *dominant eucalypt*, *non-eucalypt species*, *geology*, *aspect*, and *forest stage*.

The environmental variables are explained in Table 6.1. Coarse woody debris volumes were calculated from a line intersect transect (running 100 m north to south and 100 m east to west to form a cross; Chapter 5) by measuring the diameter and length of each log that intersected the transect line and applying the Van Wagner formula (Van Wagner, 1968).

The environmental variables *geology*, *forest class*, *broad forest class*, *age of regenerating forest*, *forest stage*, forest regenerating from silviculture or natural disturbance (*Rgr*, *Rgen* or *Mat/Rgr*) and *most recent fire* were derived from Forestry Tasmania's GIS data. The FT database 'broad forest class' and the sub-categorical 'forest classification system', which encompasses all the study area, is based on on-ground forest inventories. The classification system includes

categorical vegetation attributes and is explained in Chapter 5. Maps were produced from the GIS database to obtain data for *distance to nearest river* (in kilometres), the *forest stage*, regen or regrowth forest (*Rgr*, *Rgen* or *Mat*; see Table 6.1), *most recent fire* (wildfires), *broad forest class* and *forest class* and *geology* at each site (Figure 6.1). Forest types in the study area were categorised into two types: wet sclerophyll and mixed forest. The aspect was noted on-site prior to laying out the survey transect. Cardinal points for each site were shown to be closer to north or south on the compass so only two categories for aspect were necessary: north- or south-facing.



**Table 6.1 Environmental variables used in the predictive habitat models. BRT = boosted regression trees, BGLM = boosted general linear models and GAM = generalised additive models.**

Variable name	Descriptors	Relative model	Explanation of variable and why variable was chosen
Volume of dead wood (CWD)	cubic metres per hectare	BRT BGLM	Volume of CWD ( $\text{m}^3 \text{ha}^{-1}$ ) may relate to amount of accessible habitat for saproxylic beetle.
Rgr, Rgen or Mat/Rgr	Rgr—natural regrowth element of eucalypt stand Rgen—silvicultural regeneration of eucalypt stand Mat—mature eucalypt stand	BRT BGLM	Management history may affect forest type and structure. It may also influence CWD volumes and heterogeneity.
Most recent fire	1898-1914, 1934, 1966-67, 1969-74, 1979-83, 1992-99	BRT BGLM GAM	Year of most recent fire event for each site. These years were grouped according to fire frequency occurrence over time. Fire affects forest type, structure and CWD volume and introduces charcoal to CWD.
Age of regeneration	1898 to 1999	BRT BGLM	Affects volumes and heterogeneity of CWD.
Broad forest class	See Table 5.7, Chapter 5	BRT BGLM	Broadly defines stand structural attributes which may identify current and future CWD quantity and quality.
Forest class	A numbered code used by Forestry Tasmania to identify stand structural attributes at the site-scale (Table 5.7, Chapter 5)	BRT BGLM	Identifies in detail forest-stand structural attributes which may identify current and future CWD quality and quantity.
Dominant eucalypt	Pure <i>E. obliqua</i> Pure <i>E. regnans</i> <i>E. obliqua</i> dominant <i>E. regnans</i> dominant	BRT BGLM	Describes both structure and tree species and may indicate presence of beetle preference for CWD derived from a particular eucalypt species.
Non-eucalypt species	Other dominant tree species	BRT BGLM	Identifies tree species in the forest stand other than eucalypts
Geology	Pu=Upper glaciomarine sequences of pebbly mudstone, pebbly sandstone and limestone Pt=Talus, vegetated and active Rq=Quartz sandstone Jd=Jurassic dolerite	GAM BRT BGLM	A key biophysical variable that can influence soil fertility and forest type which may relate to volume of CWD and type of CWD (tree species from which it is derived).
Aspect	North South	GAM BRT BGLM	Has the potential to affect moisture, radiation and vegetation and therefore forest type.
Distance to nearest river	Distance in kilometres to the Huon, Picton, and Arve or Weld river	GAM	May be indicative of species choosing sites based on riparian or moist environments. It may also indicate dispersal barriers.
Forest stage	Mixed forest Wet sclerophyll forest	GAM BRT BGLM	Forests may differ in structure and floristics which may directly influence quality and quantity of CWD.

### 6.2.2 Modelling procedures

#### *Boosted regression tree (BRT) models and boosted generalised linear (BGL) models*

BRT and BGL models were used to predict the presence of the study species using site-scale variables. The AIC and K-fold cross validation were used to test the validity of site-scale predictive habitat models. Detailed explanations of these techniques are provided in Section 5.2.5, Chapter 5. In brief, the contribution of a particular variable that predicts variability in presence of a beetle is termed ‘relative influence’ and is presented as a percentage (Elith *et al.* 2008). The decision to discuss the predictor variables depended on their relative contribution to the model for both BRT and BGLM. In this study, only variables with a relative influence above 1.5 were considered influential. To make the interpretation of each BRT model easier partial dependence plots were developed for the most influential six (or fewer in some cases because the model only needed <6 predictor variables to adequately predict) variables.

#### *Generalised Additive Models (GAM)*

To test the variable spatial effect of the landscape-scale variables on saproxylic beetles species presence in the study area a binomial generalised additive model was used (GAM; Hastie and Tibshirani 1990). The GAM is a semi parametric extension of the GLM that allows a mixture of parametric and semi-parametric terms to be estimated (where semi-parametric terms are fitted as smooth functions  $[f_k(x_{ki})]$  of covariate terms). GAMs were applied to the environmental variables considered to be landscape-scale descriptors (see Section 6.2.1; Table 6.1) as they are thought to be a more appropriate modelling technique at this scale and perform better than GLMs and regression tree models when used at greater spatial scales (Segurado *et al.* 2006). The following variables and their influence on the presence/absence of the study species was examined: *geology*, *forest stage*, *aspect*, *distance to closest river* and *dominant eucalypt* (Table 6.1).

The GAM is a semi parametric extension of the GLM. Where a binomial GLM takes the form:

$$y_i \sim \text{Bin}(1, \pi_i)$$

$$\text{Log}\left(\frac{\pi_i}{1 - \pi_i}\right) = \beta_0 + \beta_1 x_{1i} + \beta_2 x_{2i} + \dots \beta_m x_{mi}$$

a binomial GAM takes the form:

$$y_i \sim \text{Bin}(1, \pi_i)$$

$$\text{Log}\left(\frac{\pi_i}{1 - \pi_i}\right) = \beta_0 + f_1(x_{1i}) + \dots + f_m(x_{mi})$$

where  $f_1 \dots f_m$  are arbitrary smooth functions. Rather than estimate the regression coefficients  $\beta_0, \beta_1 \dots \beta_m$ , the GAM estimates the smooth functions  $f_1 \dots f_m$  and the intercept  $\beta_0$ .

More generally, each of the smooth  $f_k(x_{ki})$  terms may be replaced by its parametric counterpart,  $\beta_k x_{ki}$ , allowing a mixture of parametric and semi-parametric terms to be estimated.

The disadvantage of a GAM is that the smooth terms must contribute additively; there is no scope to allow for interactions between predictors. Interactions between predictors can be allowed to a limited degree by applying smooth terms in the multiple predictors,  $f_{jk}(x_{ji}, x_{ki})$ . Unfortunately, such terms require substantially more data to be reliably estimated (Wood 2006) and so their use is generally limited to very simple interactions.

Model selection began by fitting a binomial GAM that included smoothed terms for the locations of each individual found (eastings and northings), to test for the possibility that the pattern of occurrence of each study species is purely geographic and not associated with any of the predictors measured. A stepwise model selection process was then applied, based on the Akaike Information Criterion (AIC, Section 5.2.5; Chapter 5) to determine whether adding other landscape-scale descriptors would improve the predictive power of the model. If the model only selects the smooth terms eastings and northings, then the pattern of presence/absence is not strongly predicted by the site descriptors, indicating that

there may be a complex geographic pattern of beetle occurrence but the landscape-scale variables are not sensitive enough to explain this pattern.

### 6.2.3 Validation of predictive models

All models produced a receiver operator curve (ROC) with an area under the curve (AUC) value that determined model performance (Section 5.2.5, Chapter 5). It measures the ability of a model to discriminate between sites where a species is present or absent (Elith *et al.* 2008). Area under the curve is considered to be an effective indicator of predictive habitat model performance, independent of threshold probability at which the presence of the study species is accepted (Elith *et al.* 2008).

### 6.2.4 Interpreting model outputs

#### *Interpreting partial dependence plots from BRT models*

The partial dependence plots shown in Figure 6.4 to 6.9 indicate which sub-category of predictor variable is driving the influential relationship between that variable and species presence/absence that is revealed in the BRT analysis (shown in Table 6.3). For example, the BRT for *L. menalcas* included four predictor variables, with *forest class* being the best performing (Table 6.3). However, identifying which *forest class* was most influential for predicting the presence of *L. menalcas* was only possible via examining the partial dependence plot for this species. For instance, in the BRT for *L. menalcas*, the highest bars on the *forest class* plot (top left plot in Figure 6.4) align with *forest class* 2, 12, 13, and 34 and this is interpreted as follows: the probability of occurrence of *L. menalcas* increases at sites that are categorised as being *forest class* 2, 12, 13 or 34. While the initial BRT models show the most influential predictor variables for predicting presence of each species, the partial dependence plots go one step further to elucidate what predictor variable is actually likely to increase or decrease the species probability of occurrence within the study area.

Although partial dependence plots assisted in interpreting the output of the BRT model, it was difficult to easily establish patterns among species from predictor variables *forest class*, *broad forest class* and *age of regen*. For this reason, Tables 6.7 and 6.8 were constructed to readily display the overall results of the BRT analysis and display the model-determined contribution of variables to predicting species distribution more easily; this way patterns in the results of the model

outputs could be seen among species. Values of the variables that strongly predicted species presence for all species in the BRT analysis (i.e. were the most influential in the partial dependence plots, Figure 6.4 to 6.9) are highlighted in green (and classed as high, 'H'), while those of lesser influence were classed as medium or low ('M' or 'L', Tables 6.7 and 6.8). For example, the *forest class* partial dependence plot in Figure 6.4 indicates that *L. menalcas* the highest bars on the plot align with *forest class 2, 12* and *13* and are therefore represented as 'H' in Table 6.7, alternatively the lowest bar in the same plot aligns with *forest class 25* and therefore it is represented as 'L' in Table 6.7 and has the least influence on the probability of occurrence of *L. menalcas*.

#### *Interpreting model output: contour plots from GAM models*

The contour plots from the GAM allow visualisation of patterns of distribution (presence/absence of beetles across the study area in relation to the fitted predictor variables at the landscape-scale; Figures 6.10 - 6.15). The purpose of these plots is to locate areas on the GAM map where beetles are most likely to be present. Contour plots display sites where beetles were present (closed circles) and where they are not present (open circles). The colour theme of each plot is important for visualising the distribution of the species throughout the study area: the yellow shading indicates areas of high predicted presence and red indicates low predicted presence.

## 6.3 Results

### **6.3.1 The influence of site and landscape attributes on beetle presence: summary of model performance**

The predictive habitat models constructed for the six study species at site- and landscape-scales performed very well, with AUC values showing that the GAM outperformed the other models for all species (Table 6.2). However, all GAMs had an AUC of 1, indicating that caution should be taken when using these models due to the possibility that some overfitting occurred in the final model. The models should also be used with caution because the GAMs supplied little detail at the landscape-scale and presence/absence was only established within the study area and the information cannot be applied with confidence to similar forests outside this area.

Site-scale BGLM and BRT models performed well for all species, but *Lissotes cancroides* and *Dryophthorus* ECZ sp. 02 had the lowest AUC scores (indicating the models did not perform as well as for these species) and *Coripera deplanata* has the best fitted models, having the highest AUC scores for all three modelling techniques (Table 6.2). Of the two analyses conducted at the site-scale, the BGLM performed better than the BRT model (based on AUC), though the BRT model still performed well with high AUC scores (Table 6.2). Because the results of the BRT model were easier to interpret (with the aid of partial dependence plots) than those of the BGLM, and BRT fitted models were not overly complex (compare number of variables included in Table 6.3 with Table 6.4 and 6.5) more emphasis is placed on presenting and discussing the results of the BRT models.

**Table 6.2 Comparison of model performance based on the value of the Area under Curve (AUC) of the receiver operating characteristics (ROC) plots. Such high AUC values indicate that all models are robust and perform well.**

<b>Model</b>	<i>Lissotes menalcas</i>	<i>Lissotes cancroides</i>	<i>Coripera deplanata</i>	<i>Prostomis atkinsoni</i>	<i>Dryophthorus</i> ECZ sp. 02	<i>Toxeutes arcuatus</i>
BRT	0.98	0.93	1	0.95	0.93	0.99
BGLM	1	0.87	1	1	0.99	1
GAM	1	1	1	1	1	1

### **6.3.2 Influence of environmental covariates on the presence and distribution of saproxylic beetles**

#### *Forest class and age of regenerating forest*

*Forest class* and *age of regen* were the best performing predictor variables across all six species in the BRT model (Table 6.3). The contribution of these two variables was greater than 75% for all species (Table 6.3). In the BRT model all species were found in the majority of forest classes and ages of regenerating forest but there was a difference in how frequently they occurred in them (bars aligned to forest classes and age of regenerating forest in partial dependence plots in Figure 6.4 - 6.9, the higher the bar the more frequent the species is thought to be occurring). For example, probability of occurrence of all species is increased at sites with *forest class* 12, 13, 22, 26, 34, 37 and 58 (Table 6.7). Many vegetation characteristics are depicted by the seven forest classes but the two characteristics they share are the presence of a middle-aged eucalypt regrowth and a mature eucalypt element. In the BRT models all species were found in the majority of

regenerating forests of different ages. Age of regenerating forest from 1700, 1898, 1979, 1992, 1993 and 1996 increased the probability of occurrence of all six species (Figure 6.8). Similarly to the forest classes, with the exception of forests from the late 1990s, a middle-aged eucalypt regrowth and a mature eucalypt element is present at these sites.

The predictor variable *forest class* contributed to the BGLMs for all species, influencing presence or absence in each species. Many models included forest classes that were specific to only one or two species, with very few forest classes shared across all species (Table 6.4 and Table 6.5). For example, *forest class 14* was the most influential in predicting presence in the *L. cancroides* BGLM but was not included in the BGLM of other species (Table 6.4) and *forest class 25* was ranked highly in *P. atkinsoni*, *Dryophthorus* ECZ sp 02 and *T. arcuatus* BGLMs because it was a good predictor of absence (Table 6.5). The predictor variable *age of regen* contributed to the models of many species with most BGLMs including a different *age of regen* predictor variable in each model, the exception was *age of regen 1979* which was included in the BGLM models to predict presence of *L. menalcas*, *P. atkinsoni* and *Dryophthorus* ECZ sp 02.

Overall, at the site-scale, the BGLMs were quite different for each species but some predictor variables were shared between the BGLM and BRT models. Patterns were more readily observed in the BRT models with many species sharing the same forest classes and ages of regenerating forest. In general, the results suggested that probability of occurrence of all species in the study area increases when one or more of the following elements are present in the forest stand: a mature eucalypt element, no mature eucalypt but tall dense middle-aged regrowth and conversely young regenerating forest from timber harvesting.

#### *Volume of CWD*

The predictor variable CWD made a comparatively minor contribution to a model (Table 6.3), and was not included in the BRT models developed for *Dryophthorus* ECZ sp. 02 and *T. arcuatus*. For the remaining species, the model identified a threshold figure of approximately 350 m<sup>3</sup> ha<sup>-1</sup> of CWD for predicting species presence in the study area (Figures 6.4 - 6.7).

### *Geology*

Results of site-scale (BRT and BGLM) analyses indicated the underlying bedrock in the study area predicted presence and absence of some species. In the BRT models the predictor variable geology was only influential in the model for *L. menalcas* (Table 6.3), where probability of occurrence decreased on sites with underlying bedrock of sandstone/quartzite (Rq) (Figure 6.4). The BGLM included geology in many models but in most cases they were ranked poorly (seventh in the BGLM for *L. menalcas* and ninth for *T. arcuatus*; Table 6.5).

The landscape-scale (GAM) analyses showed that the underlying bedrock in the study area predicted the presence and absence of five species (not *P. atkinsoni*) in varying ways. *Dryophthorus* ECZ sp. 02 occurred more frequently at sites where the underlying bedrock was composed of talus (Pt), mudstone (Pu) and particularly sandstone/quartzite (Rq) (Table 6.6, Figure 6.1 and 6.14). Meanwhile, *T. arcuatus* and *L. menalcas* occurred with greater probability in sites where the underlying bedrock was composed of talus (Figure 6.1, 6.10 and 6.15), and *L. menalcas* with far lower probability where the underlying bedrock was composed of mudstone (Table 6.6; Figure 6.1 and 6.10). In addition, *L. menalcas* was less common in sites with a sandstone/quartzite, glaciomarine sandstone, or mudstone bedrock explaining a decrease in the potential to locate *L. menalcas* in regions where these substrate types dominated (i.e. the north-west; Table 6.6, Figure 6.1, 6.7 and 6.10).

### *Aspect, forest stage and most recent fire*

Results of the GAM analysis revealed that at the landscape-scale the occurrence of all five of the six study species was significantly predicted by variation in geology, forest stage, most recent fire and aspect (Table 6.6). However, for *P. atkinsoni* the model performed best with only the study area included in the model (easting and northing), indicating that no landscape-scale variable was any better at predicting presence than location on the map. The occurrence of both *L. cancroides* and *C. deplanata* was strongly predicted by the aspect of the site, with *C. deplanata* apparently preferring north-facing sites (as the few sites where it was absent faced south), while *Lissotes cancroides* was less likely to be found on south-facing slopes (Table 6.6, Figure 6.2, 6.11 and 6.12). Results showed that wet sclerophyll forest increased the likelihood of locating *L. cancroides* and *L. menalcas* (Table 6.6).



Fire had a negative impact on the presence/absence of *T. arcuatus*, with results showing this species was less likely to be found in areas affected by the fires that burnt the study area in the late 1970s to 1990s and 1934 (Table 6.6). These fires were most prevalent in the mid-section of the plot, running in a south-west to north-east direction (Figure 6.2 and Figure 6.15).

**Table 6.3 Most influential predictor variables (and their % contribution to the model) included in the BRT model across all species. The ranked performance of a variable for each species is included in brackets ('0' denotes a predictor variable that was not included in the model) e.g. *forest class* predictor variable for *Lissotes menalcas* is 50.7% and since it has the highest value it is ranked (1), the second most influential predictor variable being *broad forest class* at 42.63(2). Figures 6.4-6.9 indicate which sub-categories for each variable included here in these models are most influential. *Forest class* is shown to be the most influential predictor variable but a multitude of forest classes are the reason for this e.g. *forest class 2, 12 and 13* etc are the most influential predictor variables in the BRT model for *L. menalcas* (Figure 6.4).**

Variable	<i>Lissotes menalcas</i>	<i>Lissotes cancroides</i>	<i>Coripera deplanata</i>	<i>Prostomis atkinsoni</i>	<i>Dryophthorus</i> ECZ sp. 02	<i>Toxeutes arcuatus</i>
Forest class	50.7(1)	38.96(1)	50.97(1)	68.23(1)	78.43(1)	55.16(1)
Broad Forest class	0	12.46(3)	8.5(3)	5.38(3)	0	0
Age of regen	42.63(2)	34.78(2)	32.21(2)	23.78(2)	20.3(2)	44.11(2)
CWD	2.24(3)	6.26(4)	2.61(5)	1.77(4)	0	0
Geology	1.86(4)	0	0	0	0	0
Dominant eucalypt	0	5.06(5)	0	0	0	0
Rgr/Rgen	0	0	4.77(4)	0	0	0

**Table 6.4 Top: BGLM variables predicting the presence of each species. The coefficients (value of relative influence) are derived from the AIC. The ranked performance of a variable for each species is included in brackets ('0' denotes a predictor variable that was not included in the model).**

Variable	<i>Lissotes menalcas</i>	<i>Lissotes cancroides</i>	<i>Coripera deplanata</i>	<i>Prostomis atkinsoni</i>	<i>Dryophthorus ECZ sp. 02</i>	<i>Toxentes arcuatus</i>
Age of regen 1898	0	0	0	0	0	0.46(4)
Age of regen 1979	0.26(1)	0	0	0.79(2)	0.26(2)	0
Age of regen 1993	0	0	0	0	0	2.29(8)
Dominant eucalypt pure <i>E. regnans</i>	0.84(2)	0	0	0	0	0
Forest class 14	0	0.46(1)	0	0	0	0
Forest class 18	0	0	0	0	0	0.21(1)
Forest class 22	0	0	0	0	0	0.33(3)
Forest class 34	0	0	0	0	1.5(5)	0
Forest class 38	0	0	0	0	0	1.86(7)
Forest class 58	0	0	0	0	0.12(1)	0
Geology Pu	0	0	0.66(3)	0	0	0
Geology Pt	0	0	0	0	0.42(3)	1.36(6)
Geology Rq	0	0	0	0	0	0.24(2)
Mature and regrowth	0	0	0.32(2)	0	0	0
Mature	0	0	0	0	0	0.56(5)
Broad forest class PURgroE	0	0	0.11(1)	0	0	0
Dominant eucalypt pure <i>E. obliqua</i>	0	0	0	0	0.47(4)	0
CWD m <sup>3</sup> ha <sup>-1</sup>	0	0	0	0.0003(1)	0	0

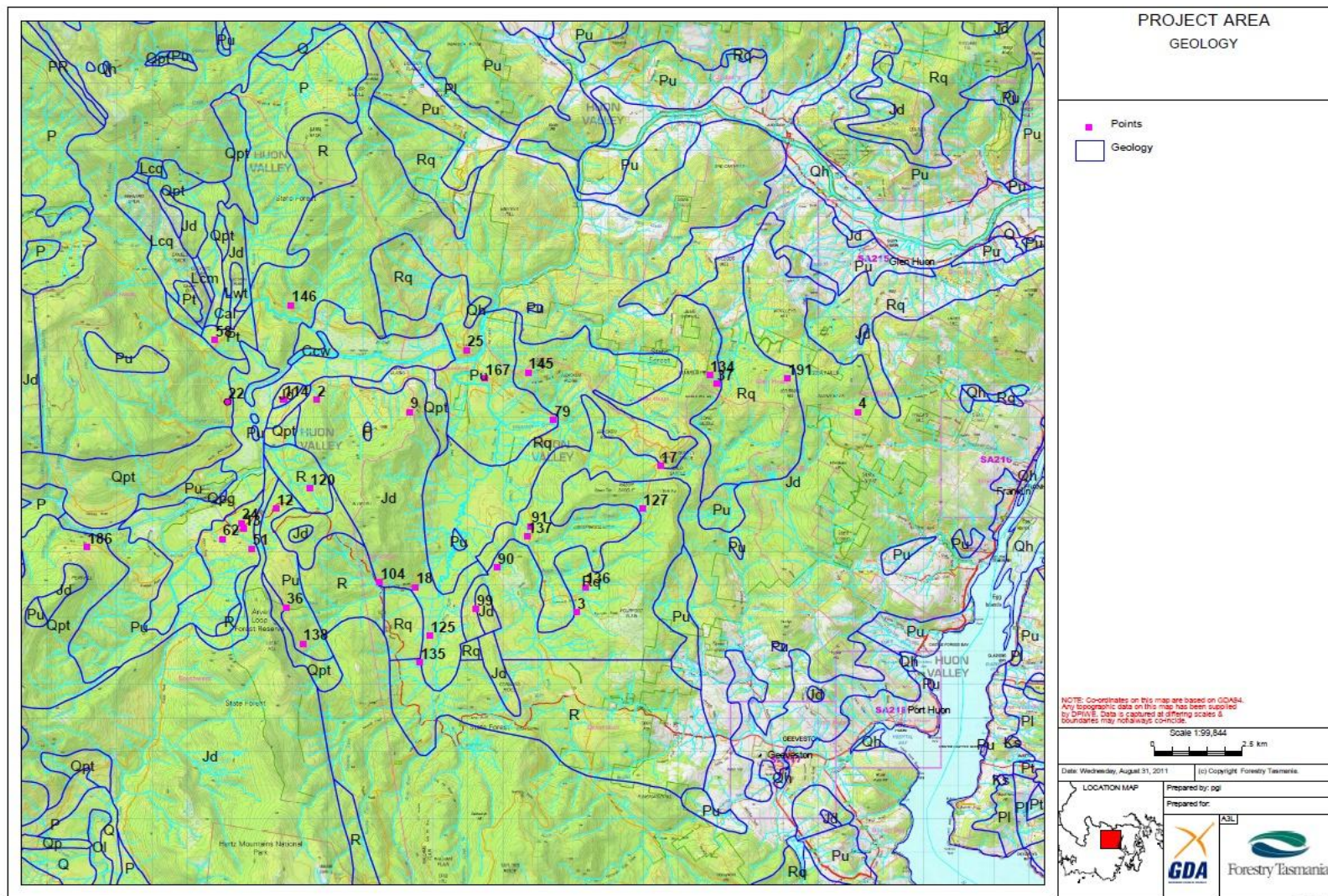
**Table 6.5 BGLM variables predicting the absence of each species. The coefficients (value of relative influence) are derived from the AIC. The ranked performance of a variable for each species is included in brackets i.e. *Age of regen 1999* is ranked number one for predicting species absence so it is shown as (1). ‘0’ denotes a predictor variable that was not included in the model.**

Variable	<i>Lissotes menalcas</i>	<i>Lissotes cancroides</i>	<i>Coripera deplanata</i>	<i>Prostomis atkinsoni</i>	<i>Dryophthorus</i> ECZ sp. 02	<i>Toxeutes arcuatus</i>
Age of regen 1999	-3.74(1)	0	0	0	0	0
Age of regen 1983	-3.25(3)	0	0	0	0	0
Age of regen 1982	0	0	0	0	-2.55(3)	0
Age of regen 1969	02.77(4)	0	0	-2.43(3)	-1.52(6)	0
Age of regen 1967	0	0	0	0	0	-0.1(6)
Age of regen 1966	0	-2.34(2)	0	-0.75(6)	0	0
Age of regen 1934	0	0	-0.57(3)	0	-0.05(9)	-1.67(4)
Age of regen 1914	-2.6(5)	0	-3.16(2)	0	0	-2.5(1)
Forest class 12	0	0	0	0	-2.22(4)	0
Forest class 20	0	0	0	-2.48(2)	-1.52(6)	-2.26(3)
Forest class 25	-3.37(2)	0	0	-3.46(1)	-2.6(1)	0
Forest class 26	0	0	0	0	0	-0.57(8)
Forest class 37	0	0	0	0	0	-0.31(10)
Forest class 38	0	0	0	0	-2.11(5)	0
Forest class 54	-1.01(6)	0	-3.25(1)	-1.6(4)	0	0
Forest class 58	0	0	0	0	0	-1.02(5)
Broad forest class MEFWoutRgro	0	-0.12(4)	0	0	-1.5(7)	0
Broad forest class MEWARgen	0	0	0	-0.95(5)	-0.92(8)	0
Broad forest class ER 1980-1999	0	0	0	0	0	-2.28(2)
Geology Rq	-0.63(7)	0	0	0	0	0
Geology Pu	0	0	0	0	0	-0.29(9)
Mature and regrowth	0	-2.47(1)	0	0	-2.57(2)	-0.73(7)
Regrowth	0	0	-0.39(4)	0	-0.03(10)	0
Dominant eucalypt pure <i>E. regnans</i>	0	-1.27(3)	0	-0.16(7)	0	0
Aspect South	0	0	-0.29(5)	0	0	0

**Table 6.6 Top: GAM variables associated with the presence of each species, that is, increased values of these variables are associated with increased likelihood of presence. The table shows the model coefficient (number in brackets indicate variable that was used by the model to improve presence/absence prediction i.e. (1) is the variable that performed the best in the model), and the Z-score and the P-value from the regression summary table. Bottom: GAM variables associated with the absence of each species.**

Variable	<i>Lissotes menalcas</i>			<i>Lissotes cancroides</i>			<i>Prostomis atkinsoni</i>			<i>Dryophthorus ECZ sp. 02</i>		
	c	z	p	c	z	p	c	z	p	c	z	p
Geology Pt	19.30(2)	7.12e-06	1	0	0	0	0	0	0	127.50(3)	1.9e-06	1
Geology Pu	0	0	0	0	0	0	0	0	0	26.30(2)	0.03	0.97
Geology Rq	0	0	0	0	0	0	0	0	0	18.50(1)	0.125	0.9
Forest stage wet sclerophyll	17.35(1)	0.51	0.60	253 (1)	1.42e-4	1	0	0	0	0	0	0
Easting and northing	0	0	0	0	0	0	13.06(1)	0.24	0.80	0	0	0

Variable	<i>Lissotes menalcas</i>			<i>Lissotes cancroides</i>			<i>Coripera deplanata</i>			<i>Toxeutes arcuatus</i>		
	c	z	p	c	z	p	c	z	p	c	z	p
Geology Pu	-114.7(2)	-6.16 e-06	1	0	0	0	0	0	0	0	0	0
Geology Rq	-169.9(1)	-9.13e-06	1	0	0	0	0	0	0	0	0	0
Aspect south	0	0	0	-1641(1)	-3.31e-04	1	-365.2(1)	-1.58e-05	1	0	0	0
Most recent fire 196601967	0	0	0	0	0	0	0	0	0	-90(5)	-1.69e-06	1
Most recent fire 1969-1974	0	0	0	0	0	0	0	0	0	-112.1(4)	-2.89e-06	1
Most recent fire 1979-1993	0	0	0	0	0	0	0	0	0	-253.3(1)	-5.17e-06	1
Most recent fire 1898-1914	0	0	0	0	0	0	0	0	0	-233.8(2)	-4.27e-06	1
Most recent fire year 1934	0	0	0	0	0	0	0	0	0	-211.8(3)	-5.46e-06	1



**Figure 6.1 Map of underlying bedrock (geology) within the study area (purple point and number represents a site). Geology types referred to in this study are: Pu=Upper glaciomarine sequences of pebbly mudstone, pebbly sandstone and limestone, Pt=Talus, vegetated and active, Rq=Quartzite and sandstone, Jd=Jurassic dolerite.**



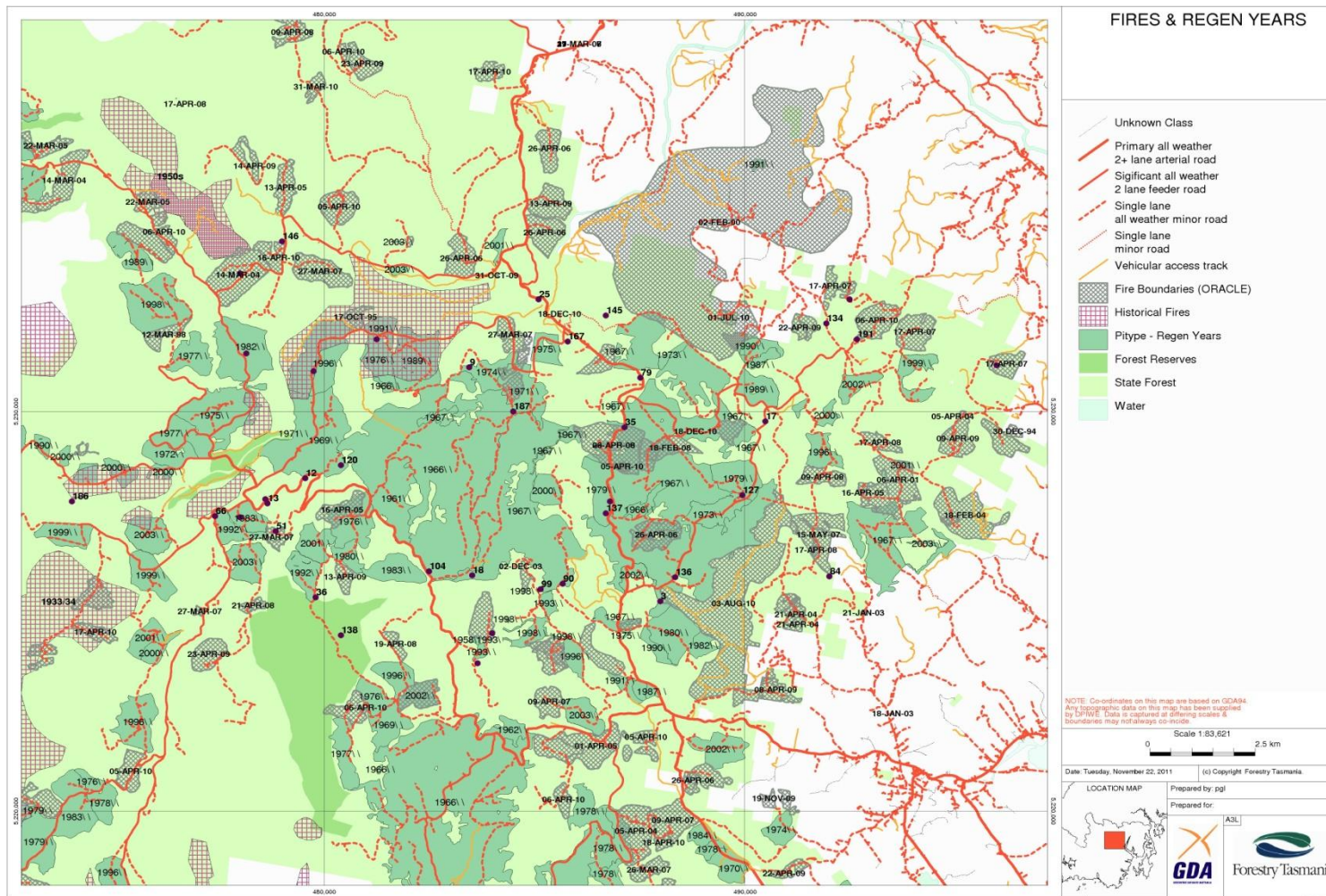


Figure 6.2 Map of study area showing historical wildfires (Table 6.1) and Forestry Tasmania's regenerating burns.

### 6.3.3 Forest class and age of regenerating forest: an example of autocorrelation

The same four elements that the *forest class* variables in the BRT indicated as important when predicting presence/absence fell within the respective *broad forest class*. In other words, broad forest classes that predicted presence/absence directly related to the forest classes that predicted the same presence/absence, yet both were necessary as performance of the model dramatically decreased when one was taken out.

When comparing the influence of *forest class* and *age of regen* (age of regenerating forest) it is apparent that some of these variables perform well for all species and those variables are highlighted in green (Table 6.7 and 6.8). The BRT model performed well when *age of regen* and *forest class* are included. This may be because these variables are closely linked; however, when one of the two is dropped from the analysis the models perform quite poorly. Thus, the model cannot distinguish *forest class* and *age of regen*, and these are both good predictors so they both appear. For example, suppose we had a simple regression situation where only  $X_1$  is actually important,

$$y = ax_1 + b + e$$

but  $X_1 = X_2$ , so whether a model is fitted with  $X_1$  or  $X_2$  it will make no difference. If we were to perform a boosted tree model, about half the time it will choose  $X_1$  and half it will choose  $X_2$ . In this case, *age of regen* and *forest class* are similar: sometimes the model chooses one, sometimes it chooses the other, but each of these variables is interpreted differently. Because they are both considered equally by the model, if one of these variables is dropped then the model loses a significant amount of contribution and performance is compromised.

In general terms the important predictor variables seem to be *forest class* and *age of regen*. All species are found in an array of both these site predictors, indicating that at the site-scale these beetles are not restricted because of specific features of the site, but some specific forest classes and ages of regenerating forest increase the probability of presence of beetles (Table 6.7 and 6.8). This is likely to be due to the characteristics of the forest stand and how they are formed (e.g. fertility of soils and fire frequency); a concept that will be discussed in Section 6.4.

**Table 6.7 Summary of *forest class* variables from the partial dependence plots (BRT). The effect of variables on species presence is shown using H, M and L (H = high effect on the response, medium effect and L = little effect). Forest classes highlighted in green are the best performing predictor variables across all species.**

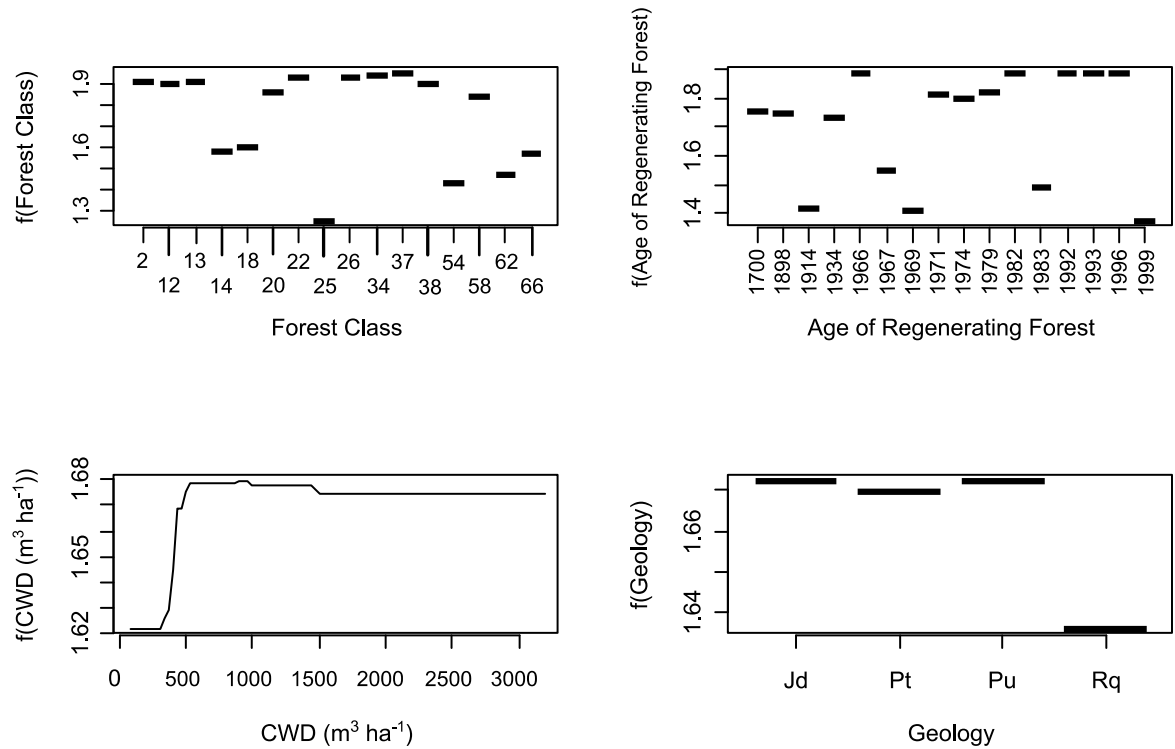
Forest class	<i>Lissotes menalcas</i>	<i>Lissotes cancroides</i>	<i>Coripera deplanata</i>	<i>Prostomis atkinsoni</i>	<i>Dryophthorus ECZ sp. 02</i>	<i>Toxeutes arcuatus</i>
2	H	L	L	H	L	M
12	H	H	H	H	M	H
13	H	H	H	H	H	H
14	M	H	M	H	M	M
18	M	M	H	L	L	H
20	H	H	H	M	M	M
22	H	H	H	H	H	H
25	L	H	L	L	M	M
26	H	H	H	H	H	M
34	H	H	H	H	H	H
37	H	H	H	H	H	M
38	H	H	H	H	L	H
54	M	H	H	M	M	H
58	H	H	H	H	H	M
62	M	H	H	H	M	L
66	M	H	H	H	H	L

**Table 6.8 Summary of *age of regen* variables from the partial dependence plots (BRT). The effect of variables on species presence is shown using H, M and S (H = high effect, M = medium effect, L = small effect). Best performing predictor variables are shown in green**

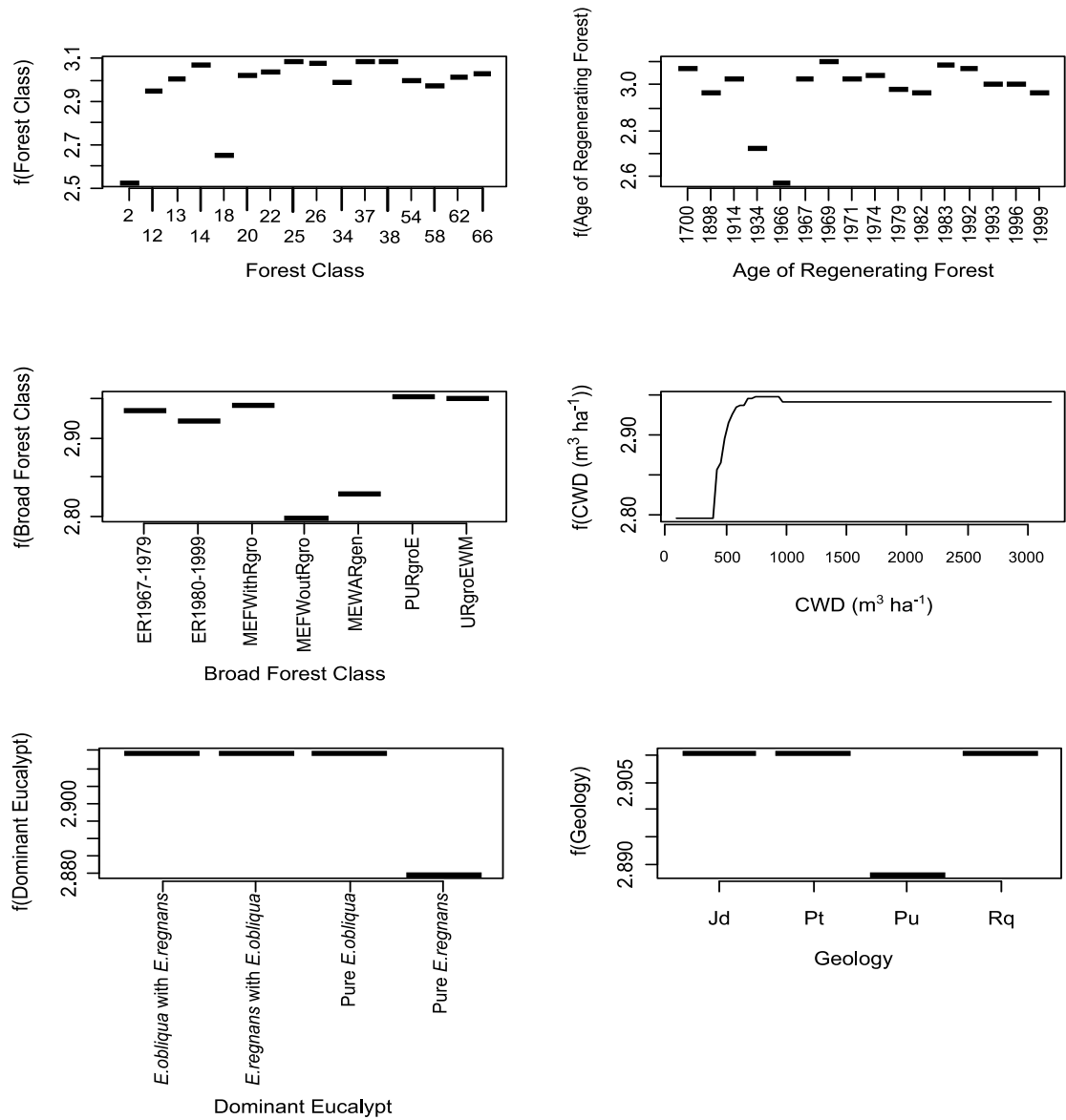
Age of regen	<i>Lissotes menalcas</i>	<i>Lissotes cancroides</i>	<i>Coripera deplanata</i>	<i>Prostomis atkinsoni</i>	<i>Dryophthorus ECZ sp. 02</i>	<i>Toxeutes arcuatus</i>
1700	H	H	H	H	M	H
1898	H	H	H	H	H	H
1914	L	H	L	H	H	M
1934	H	L	L	H	L	L
1966	H	L	H	L	M	H
1967	L	H	H	L	L	H
1969	L	H	H	L	M	H
1971	H	H	H	H	M	M
1974	H	H	H	L	L	M
1979	H	H	H	H	H	H
1982	H	H	H	H	M	M
1983	L	H	H	H	H	M
1992	H	H	H	H	H	M
1993	H	H	H	H	H	H
1996	H	H	H	H	H	M
1999	L	H	H	H	H	M



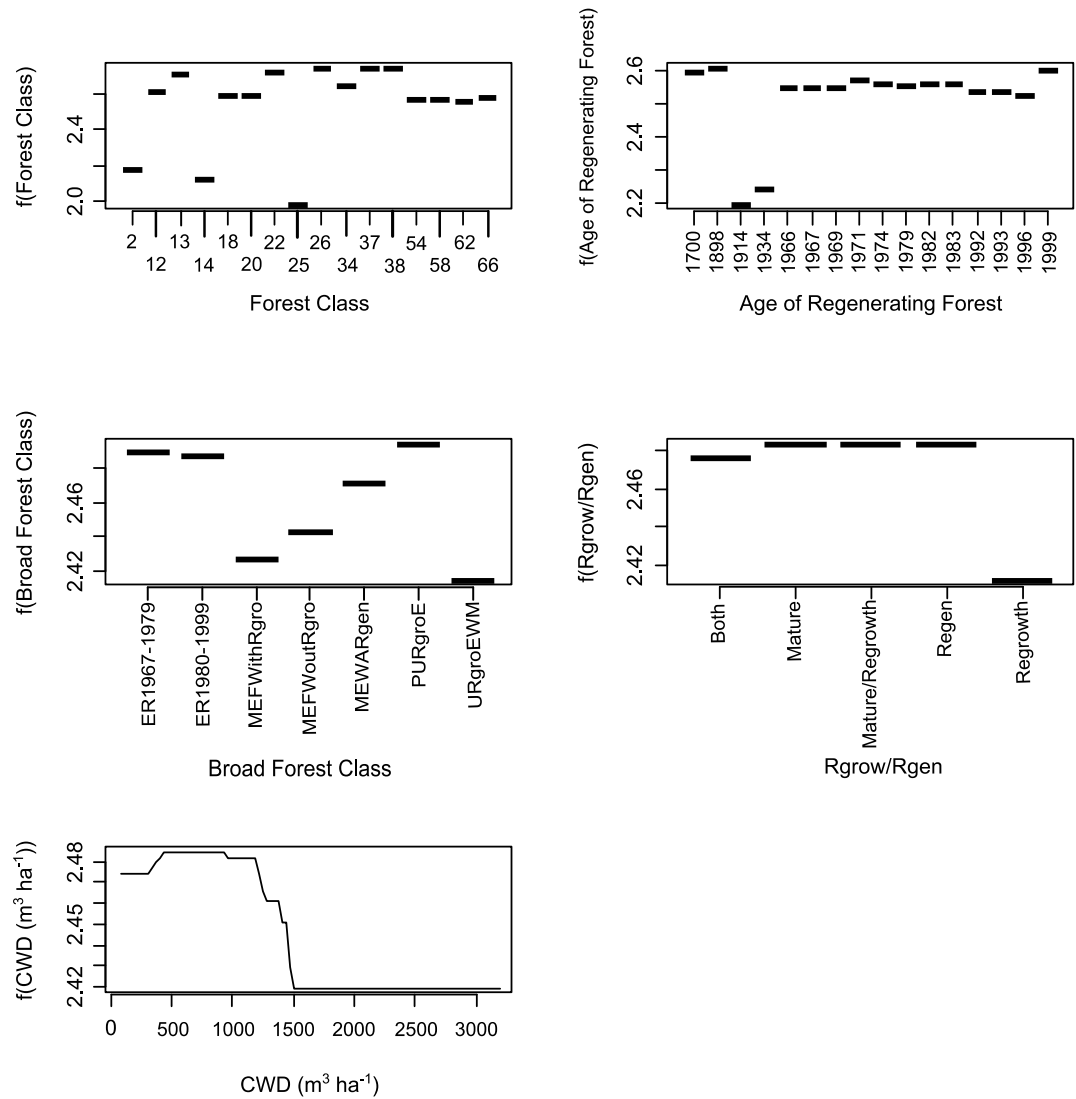
Site-scale partial dependence plots (BRT)



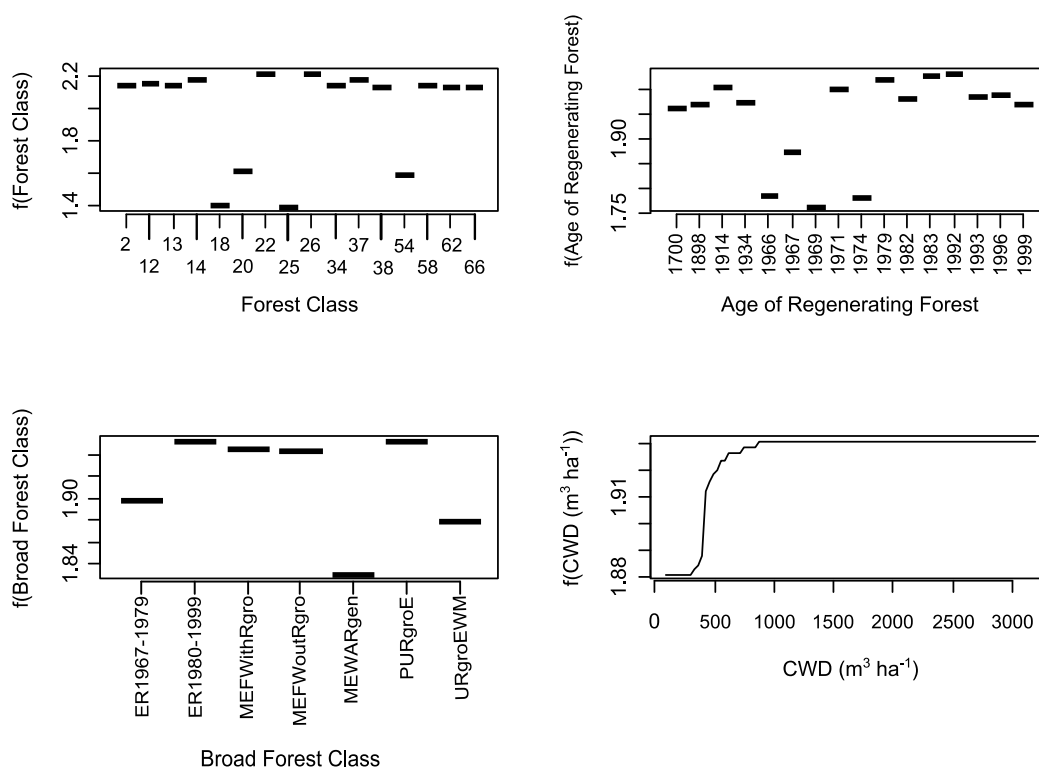
**Figure 6.4** Functions fitted for the four most influential predictor variables in the boosted regression tree model (BRT) relating the probability of occurrence of *Lissotes menalcas* to its CWD environment. For an explanation of the variables refer to Table 6.1 and Table 5.7 (Chapter 5). The probability of species occurrence increases with the increasing height of a bar or line on the plot. For example, in the *forest class* plot, the probability of finding *L. menalcas* in *forest class* 25 is low. The partial dependence plot for CWD shows the line on the plot spikes at approximately  $350 \text{ m}^3 \text{ha}^{-1}$ , which means that in this analysis the probability of presence of *L. menalcas* increase at sites where volumes of CWD are  $350 \text{ m}^3 \text{ha}^{-1}$  or greater.



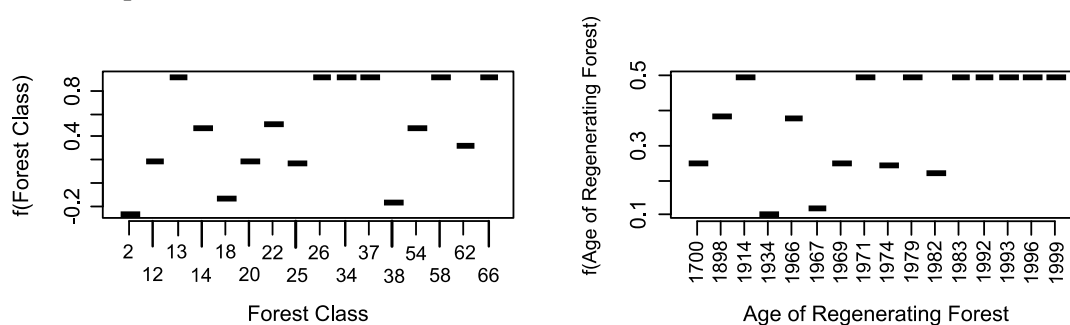
**Figure 6.5** Functions fitted for the six most influential predictor variables in the boosted regression tree model (BRT) relating the probability of occurrence of *Lissotes cancrivorus* to the landscape. For an explanation of the variables refer to Table 6.1 and Table 5.7 (Chapter 5). The probability of species occurrence increases with the increasing height of a bar or line on the plot.



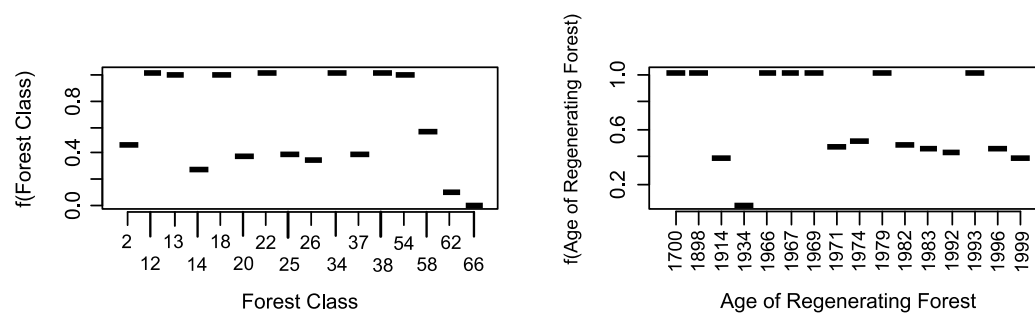
**Figure 6.6** Functions fitted for the five most influential predictor variables in the boosted regression tree model (BRT) relating the probability of occurrence of *Coripera deplanata* to the landscape. For an explanation of the variables refer to Table 6.1 and Table 5.7 (Chapter 5). The probability of species occurrence increases with the increasing height of a bar or line on the plot.



**Figure 6.7** Functions fitted for the four most influential predictor variables in the boosted regression tree model (BRT) relating the probability of occurrence of *Prostomis atkinsoni* to the landscape. For an explanation of the variables refer to Table 6.1 and Table 5.7 (Chapter 5). The probability of species occurrence increases with the increasing height of a bar or line on the plot.



**Figure 6.8** Functions fitted for the two most influential predictor variables in the boosted regression tree model (BRT) relating the probability of occurrence of *Dryophthorus ECZ* sp. 02 to the landscape. For an explanation of the variables refer to Table 6.1 and Table 5.7 (Chapter 5). The probability of species occurrence increases with the increasing height of a bar or line on the plot.



**Figure 6.9** Functions fitted for the two most influential predictor variables in the boosted regression tree model (BRT) relating the probability of occurrence of *Toxeutes arcuatus* to the landscape. For an explanation of the variables refer to Table 6.1 and Table 5.7 (Chapter 5). The probability of species occurrence increases with the increasing height of a bar or line on the plot.

*Landscape-scale contour plot (GAM)*

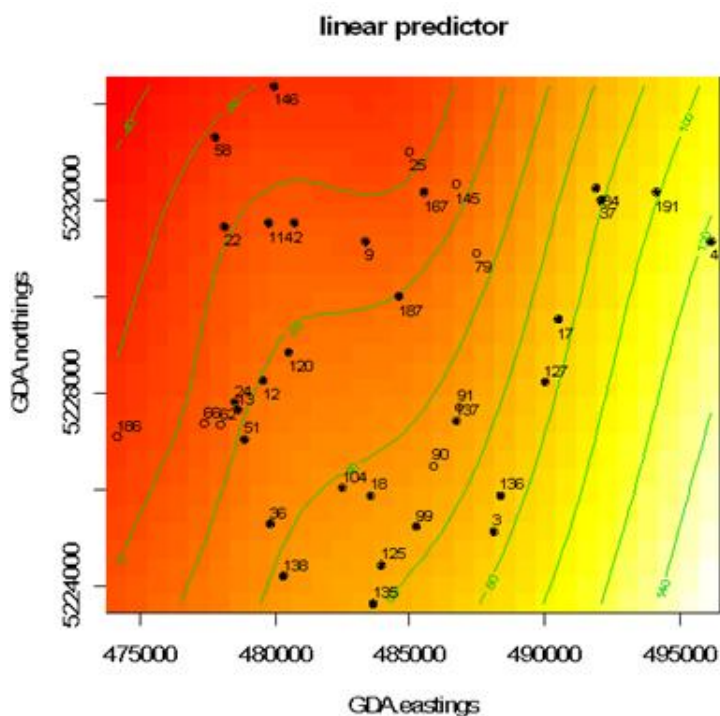


Figure 6.10 Contour plot of the smooth surface (easting and northing) for the distribution of *Lissotes menalcas* (based on presence/absence data) using the predictor variables geology and forest stage. Showing sites that detected (closed circles) and did not detect (open circles) *Lissotes menalcas*. Figure 6.1 shows a map of the geology of the study area for site comparison. Yellow shading indicates high predicted presence and red indicates low predicted presence of *L. menalcas*.

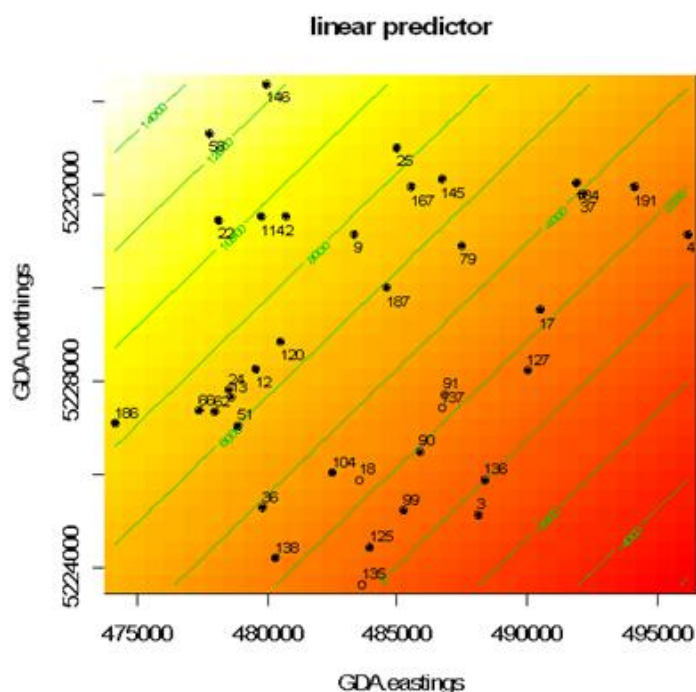


Figure 6.11 Contour plot of the smooth surface (easting and northing) for distribution of *Lissotes cancrroides* using predictor variables *forest stage* and *aspect*. Yellow shading indicates high predicted presence and red indicates low predicted presence of *L. cancrroides*.

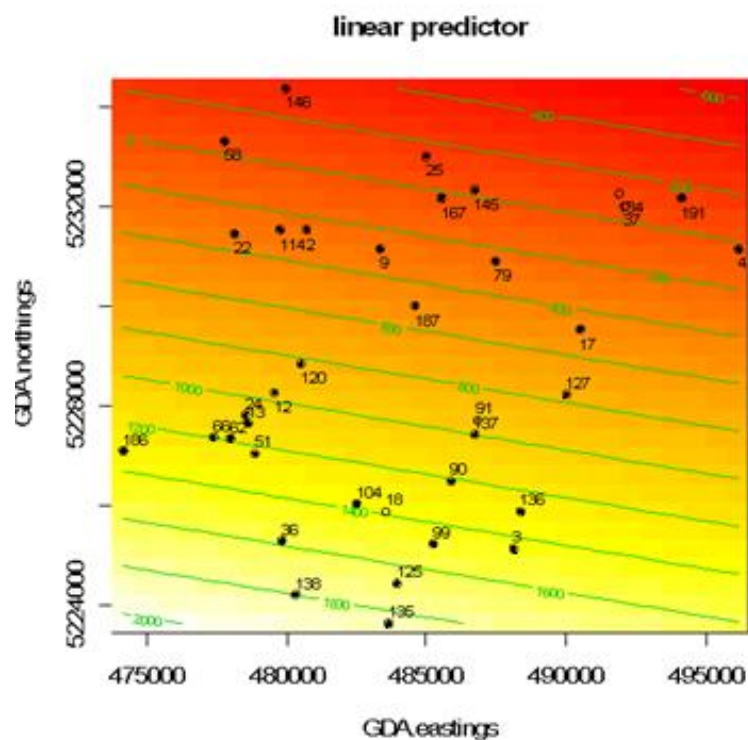


Figure 6.12 Contour plot of the smooth surface (easting and northing) for distribution of *Coripera deplanata* using predictor variable *aspect*.

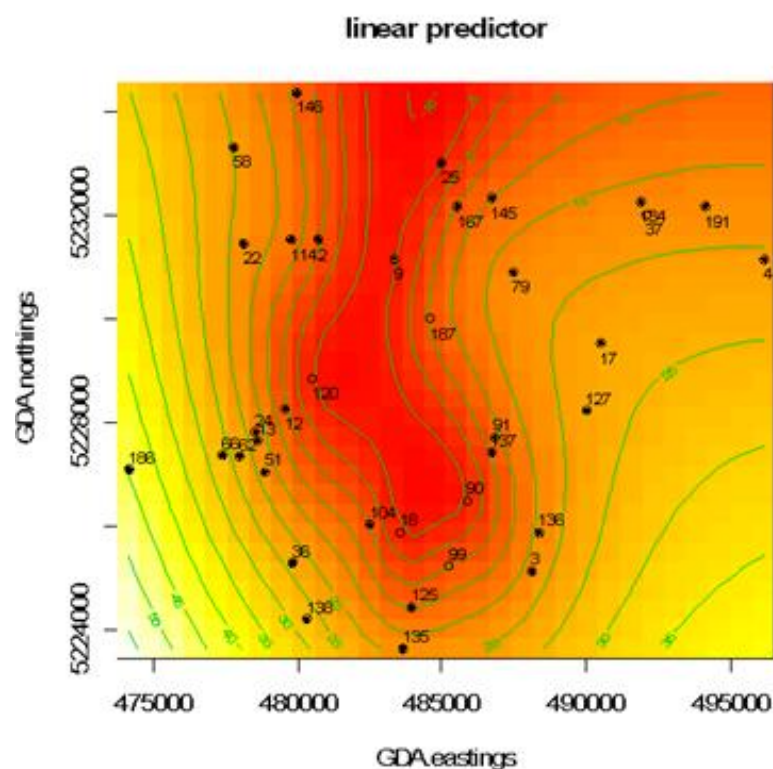
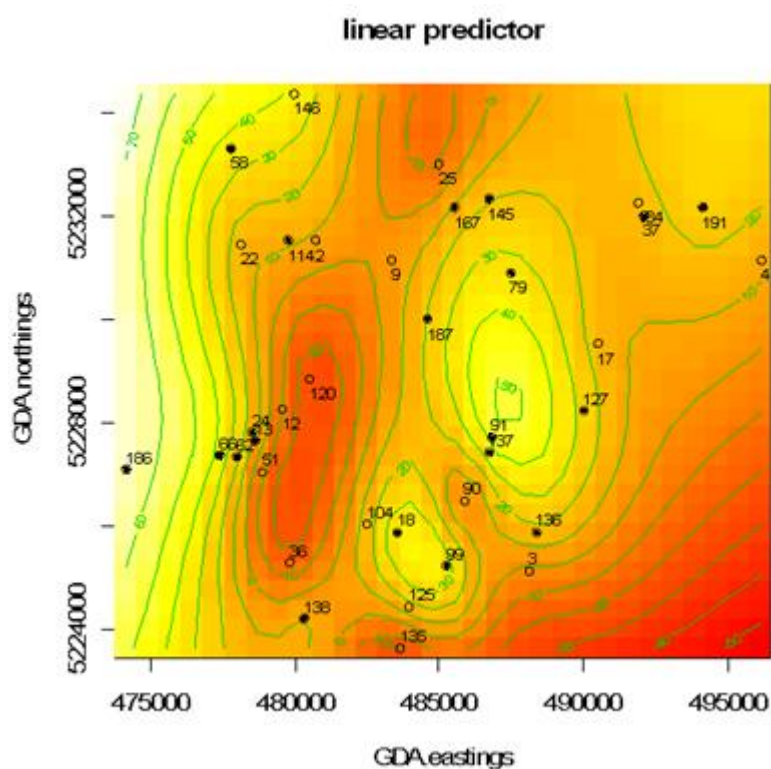
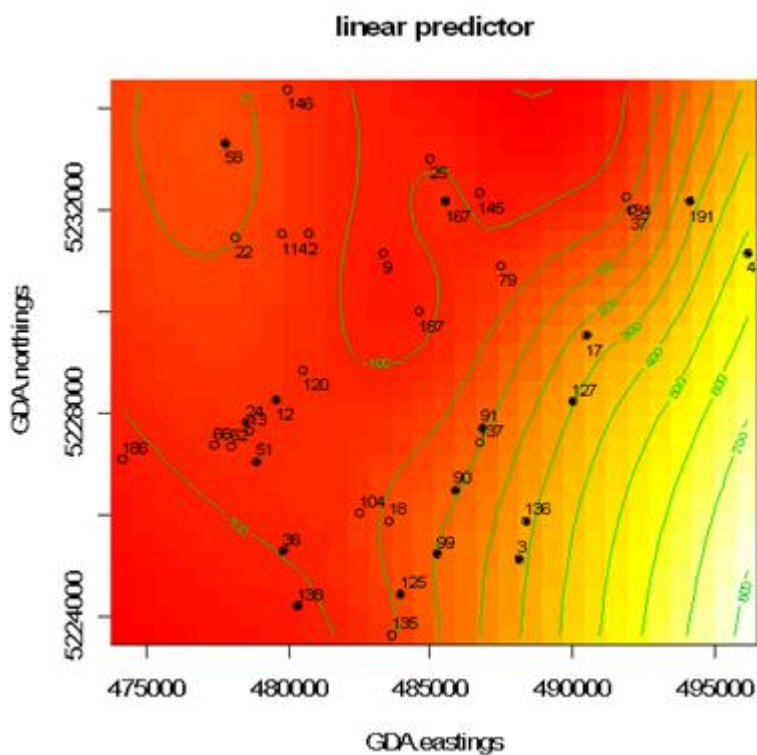


Figure 6.13 Contour plot of the smooth surface (easting and northing) for distribution of *Prostomis atkinsoni* with latitude and longitude as the predictor variables.



**Figure 6.14** Contour plot of the smooth surface (easting and northing) for distribution of *Dryophthorus* ECZ sp. 02, including the predictor variable *geology*.



**Figure 6.15** Contour plot of the smooth surface (easting and northing) for distribution of *Toxotes arcuatus*, including the predictor variable *most recent fire year*. Figure 6.2 shows a map of the fire history of the study area for site comparison.

## 6.4 Discussion

Understanding the way an organism selects its habitat is useful for understanding how it might respond to natural or anthropogenic alterations of habitat. In this study specific habitat attributes have been sampled at the site- and landscape-scale and some of these attributes have allowed predictions (via predictive habitat models) to be made as to where the six saproxylic beetles were expected to occur within the study area. The main findings suggest models which include environmental predictor variables that comprise multi-aged stands, providing CWD at varying ages, decay stages and diameters best predict the presence of the study species, probably because they assure continual replenishment of CWD habitat.

The BRT and BGL model revealed that the presence of beetles was largely influenced at the site-scale by predictor variables *forest class* and *age of regeneration*, while *broad forest class*, *volume of CWD* and *geology* were influential in some BRT models. The BRT models indicated that many species shared forest class types which increased their probability of occurrence, however, the forest classes used in the BGLMs were mostly species-specific. At the larger landscape-scale (GAM) the presence of each beetle was explained by one or more of the following: *geology*, *forest stage*, *aspect* and *most recent fire*. Predictor variables at the site-scale (especially *forest class* and *age of regen*) were found to be particularly strong predictors of species presence. Furthermore, many of these variables can be assigned to a broad forest class, demonstrating that these beetles are more likely to be present at sites where particular management (and disturbance) histories have produced structurally complex forests.

### 6.4.1 Understanding the habitat preferences of saproxylic beetles

To date, knowledge of ecological preferences of this group of saproxylic beetles has been limited to an understanding of their presence in small and large diameter *E. obliqua* CWD and rotten-wood types (Yee 2005). Results presented in Chapter 5 of this thesis, complement and extend the results of Yee (2005) to show that, at a fine-scale, these beetles exhibit species-specific preferences for certain tree species, decay stages and particular suites of rotten-wood types. The results of this Chapter, further extend our knowledge of the habitat requirements of these six



saproxylic species at greater spatial scales, and reveal that structural attributes of forest stands may be the key to predicting presence at these scales.

*Habitat requirements of six saproxylic beetles within wet-eucalypt production forest in Tasmania*

The results of this study showed that predictor variables *forest class*, and *age of regen* (age of regenerating forest) explain a significant component of the variation in species presence within the study region at the site-scale. These predictor variables depict the structural attributes of a site that are derived from differing management histories, and thus highlight the role of management practices in mediating the probability of occurrence and distribution of this group of beetles within the study area. All species preferred sites with a mature eucalypt component and a middle-aged regrowth element (regrowth being tree growth created by anything other than forestry activities). Features such as mature eucalypt habitat and middle-aged regrowth promote multi-aged vegetation elements that appear favourable to this group of beetles. Stands with regrowth elements exhibit greater structural complexity than those forests with no regrowth (Wardlaw *et al.* 2012). Structurally complex forests contain multi-aged stands that provide CWD at varying ages, decay stages and diameters, assuring continual replenishment of CWD and therefore continuation of habitat for saproxylic beetles. Moreover, trees from multiple cohorts with snags and other features are thought to enhance the dispersal and persistence of forest-dwelling species, and to help a logged forest return to suitable habitat by facilitating the nutrient cycle through feeding in dead wood (Lindenmayer *et al.* 2006). For these reasons, the structural complexity of a forest may be one of the major driving forces maintaining the persistence of saproxylic beetle because structurally complex forests ensure continuous dead-wood habitat (Økland *et al.* 1996; Maleque *et al.* 2006; Müller *et al.* 2008). In this study, forest regrowth was primarily the result of wildfires that encompassed much of the study area at various times during the past 80 years (see Figure 6.1). While many of these wildfires were not sufficiently intense to replace the entire stand (as is evident by the presence of mature eucalypts at these sites; pers. obs.), these fires are, nonetheless, likely to have affected the availability of CWD and thus, the spatial distributions of the study species.

Old-growth forests, in which the mature eucalypt component is well-represented, are thought to support greater species diversity and abundance of saproxylic beetles than do other forest types (Martikainen *et al.* 2000; Grove 2002). Indeed, some beetle species are known to occur solely in old-growth forests (Komonen 2001). This finding, however, is not fully supported by this study because old-growth forests may not contain the structural diversity seen in middle-aged forests and it is the structural diversity which is thought to increase the study species presence. Old-growth forests by their very nature have gone largely undisturbed for long periods of time; they may not contain multi-aged stands that provide CWD at varying ages, decay stages and diameters, particularly those forests that have been undisturbed for 300 years or more. When the beetles were located at old-growth sites, they were found in CWD derived from senescing eucalypts, capable of providing large volumes of CWD habitat in one tree-fall event and although these forests are not structurally diverse and less-frequently disturbed by wildfire they are capable of providing instant large volumes of habitat that may last many decades.

It is possible that *age of regen* was the second most important predictor variable due to its close link with vegetation attributes that best predict species presence. The results of this study certainly support this finding with many regenerating forests at an age where they would have characteristics such as a mature eucalypt element and middle-aged regrowth. Interestingly, results of the BRT analysis revealed that all the species preferred regenerating forest logged during the 1990s. Prior to 1960 logging was far more selective than it is today, and prior to 1970 poorer-quality timber was not harvested as there was no pulp market. Thus historically, logging events may have had little impact on the beetles' presence. In addition, logging events that pre-date the Forest Practices Code (FPC) of 1985 (updated in 2000) were not regulated by current environmental standards (for tree harvesting or land clearing), potentially leaving more CWD on the ground pre FPC; however, this does not suggest that the implementation of the FPC had a negative impact on saproxylic beetles. Stands logged in the past (as recent as the 1990s) are likely to contain a greater volume of CWD as a result of non-commercially-viable timber being left on the forest floor. These stands will offer saproxylic species a greater amount of potential habitat, facilitating the persistence of these species in what would otherwise be unfavourable conditions (<25 year

old regenerating forest). This highlights the important role of legacy CWD in facilitating the persistence of beetles within forests until such time that the new forest stand is able to produce dead wood (Franklin *et al.* 2000). If the legacy CWD does not disappear (via decay) prior to the establishment of a stand capable of replenishing CWD then these saproxylic beetles stand a good chance at persisting in these forests (see also the discussion on the ‘lifeboat’ theory in Chapter 5).

The volume of CWD within a forest stand has been shown to be positively associated with both the abundance and diversity of saproxylic species at the site-scale (Sahlin and Ranius 2009). The results of this study lend support to this observation, showing that volume of CWD was an important predictor of occurrence for all species apart from *Dryophthorus* ECZ sp. 02 and *T. arcuatus* (for these two species only predictor variables *forest class* and *age of regen* were needed at the site-scale analyses to predict presence). Although the model identified the threshold figure of approximately 350 m<sup>3</sup> ha<sup>-1</sup> of CWD, the specific amount of CWD per hectare that provides the qualities sought after by these beetles remains unknown. Tasmania’s wet-eucalypt forests are unique both in Australia (Woldendorp *et al.* 2002) and globally for containing very high volumes of CWD (a volume of 150m<sup>3</sup> ha<sup>-1</sup> of CWD is considered high by European standards; Ehnström 2001; Jacobs *et al.* (2007); Müller and Bütler (2010)). This may be a consequence of the fact that large senescent eucalypts lose their crown and limbs in mature forests, offering a source of CWD not present in non-eucalypt forests. In addition, CWD in Tasmania’s southern wet-eucalypt forests are of large diameter, generally contain high amounts of moisture, are slow to decay, and harbour dark rotten-wood types favoured by many saproxylic beetles. These logs create a moist environment that would need a high-intensity burn to be destroyed completely, and are thus likely to protect saproxylic beetles from fire. Individual logs in these forests therefore have the potential to sustain many generations of saproxylic beetles (Grove 2002). Hence, it would be interesting to assess species richness of saproxylic beetles in Tasmania’s managed forest reserves relative to that found in harvested forests around the world.

Productivity of wet-eucalypt forests of southern Tasmania is largely dependent on the fertility of soils. Geology is a key biophysical variable influences forest type and structure due to the differing fertility of soils developed on different rock

types. The results of one GAM revealed that *L. menalcas* was more likely to be present in sites existing on Jurassic dolerite, while *Dryophthorus* ECZ sp. 02 was less likely to be found in these areas. This indicates that geology may be influencing the probability of occurrence for these species.

Many biophysical relationships at the landscape-scale involve the interplay between geology, aspect and fire, which together determine the type and composition of the forest (Jackson 1968). For example, geology helps determine the probability of fire, because less-productive forest (i.e. on sandstone) is likely to be more open, more sclerophyllous and more fire-prone, it is then a case of positive feedback. Fires can have complex consequences for forest structure and productivity depending on fire intensity and frequency. At lower intensities fires can burn patches, or scorch trunks, but leave stands largely intact, such that the volume of CWD increases immediately and over time, as the remaining trees continue to replenish the CWD pool (Gilbert 1959). At higher intensities, however, fire has the capacity to destroy an entire forest stand, destroying the existing CWD and delaying future CWD stocks for years to come. Similarly, an area of forest that has experienced repeated fires at short intervals will be structurally simple as a consequence of the loss of standing trees, and will thus also be depleted of CWD resources (Grove and Stamm 2011). In contrast, an area of forest that has not been exposed to fire for more than 300 years is likely to be structurally less complex, and contain fewer mature eucalypts, with a larger area of rainforest species. All of these changes through fire may affect the presence of saproxylic beetle species because they can alter the volume of dead wood and the tree species that comprise the CWD resources.

This study showed that both *Lissotes* species were more likely to occur in wet sclerophyll forest than mixed forest. This finding may be a consequence of the fact that more wet sclerophyll sites were surveyed (N = 25) than mixed forests sites (N = 10). Alternatively, this finding may also indicate that *Lissotes* species are dependent on greater diversity of trees than is present in mixed forest. Wet sclerophyll forests yield a more diverse eucalypt assemblage than do mixed forests and also contain a variety of non-eucalypt species, some of which are known to be associated with the presence of some saproxylic beetles. This suggestion is supported by previous work showing that *L. menalcas* occurs most

frequently in CWD derived from *Acacia melanoxylon* rather than *Eucalyptus regnans* or *E. obliqua* (Chapter 5).

Model results revealed that fire events had a negative effect on the presence of *T. arcuatus* across the study area, whether they were recent (occurred in the past 20 years) or historic (occurred more than 70 years ago). Most sites in the study area have been affected by fire within the last 70 years and some have experienced more than one fire event. The results of the study cannot answer why *T. arcuatus* is absent in areas affected by fire, but it is likely that intensity and frequency of fire may limit the availability of preferred CWD habitat i.e. it may not like to inhabit the charred CWD left on the forest floor after fire.

The aspect of a site has been shown to be strongly associated with both forest type and fire intensity in Tasmania (Kirkpatrick and Nunez 1980). Southerly facing slopes that are less exposed to sunlight than north-facing slopes, are wetter, less fire-prone and exhibit higher productivity (which may equate to higher above-ground biomass on high-fertility soils) than (Kirkpatrick and Nunez 1980) than north-facing slopes. Accordingly, most intense wildfires are driven by hot northerly or north-westerly winds in summer on the drier more sun-exposed northern slopes (Kirkpatrick and Nunez 1980). Differences in moisture content, fire intensity and insolation can influence the occurrence of saproxylic beetles, and can also mediate the volume of CWD at a site, further influencing beetle distributions.

The results of the GAM analyses revealed that the aspect of a site was the best predictor variable in the GAM for *C. deplanata* and *L. cancroides*. The models for these species suggest *C. deplanata* and *L. cancroides* are most likely present in the study area where a northerly aspect dominates, producing drier, sun-exposed conditions more prone to fire disturbance. Few studies involving saproxylic beetles have highlighted the importance of aspect. However, Meggs *et al.* (2004) developed a predictive habitat model for the threatened Tasmanian lucanid, *Hoplogonus simsoni* (a close relative of the two *Lissotes* species included in this study) and found that aspect was significantly associated with its occurrence, with beetles “consistently occurring at higher densities on slopes with southerly aspects”. It is not known why *C. deplanata* and *L. cancroides* are more sensitive to aspect but it could be due to thermal tolerance, as this has been identified in

other taxa such as voles, where suitable habitat is characterised by an aspect that minimises solar irradiance (Orrock *et al.* 2000).

#### **6.4.2 Fire, geology, aspect and forest type may interact to influence the occurrence of the study species'**

The interplay of fire history, geology, aspect and forest type, and the feedbacks in these relationships, may help to explain why some of the site-scale predictors contributed greatly in many habitat models. An example of this is the relationship between geology and forest type. In the southern wet-eucalypt forests of Tasmania, Jurassic dolerite produces fertile soils and is ubiquitous with highly productive forests (Harris and Kitchener 2005). Therefore, geology influences soil fertility which can affect what types of trees are able to grow in more or less fertile soils. In wet-eucalypt forests, fertile soils are known to produce productive forests in terms of biomass, which influences the volume of CWD. Soil fertility may also determine the presence of particular tree species, which can influence the occurrence of saproxylic species at a site (e.g. *L. menalcas* is strongly associated with *A. melanoxyton*, while *Dryophthorus* ECZ sp 02 is found exclusively in the dead wood of *E. regnans* and *E. obliqua*).

This study has revealed that, at the site-scale, *forest class* and *age of regen* (age of regenerating forest stand) are the two most influential predictors of beetle presence for all six species. However, at the landscape-scale, predictor variables of beetles' presence were largely species-specific and limited to *geology* for *L. menalcas*, *Dryophthorus* ECZ sp 02, *aspect* for *L. cancroides* and *C. deplanata* and *most recent fire* for *T. arcuatus* to explain the spatial variation of species presence/absence across the study area.

#### **6.4.3 Uncertainties with model reliability and model interpretation**

Employing a GAM at the landscape-scale produced models that appeared to perform better than those at the site- and CWD-scale (Chapter 5) but this does not mean the GAMs are accurate at predicting the distribution of the beetles across the landscape. Modelling at these larger spatial scales has identified some predictors that appear to perform well; but the models may be uninformative at greater spatial scales due to autocorrelation and overfitting. Unfortunately the methods that protect the BRT and the BGL model from overfitting are not available for GAMs and caution is therefore needed when interpreting the results

of the GAMs. It is possible that the GAMs may not be overfitting and may be accurately predicting species presence. The only way to find out how reliable the GAMs are would be to test (validate) the models with field data i.e. conducting field surveys in areas where the GAMs predict species presence/absence, but validating the models was outside the scope of this study.

While this study endeavoured to include all environmental variables likely to influence the occurrence of saproxylic species, there may be historical processes that explain species distribution across the study area that could not be measured, and were thus not included in analyses. First, the occurrence of species in the study area may be explained by palaeoecological processes operating at the landscape-scale. Such processes could include the effects of glacial forest refugia, which are believed to have an influence on species distributions in Tasmania (Kirkpatrick and Fowler 1998). The study area falls within the region that Sharples (2002) states “to be of geoconservation significance for the scientific information it contains about an early phase of southern Tasmania's Cainozoic glacial history, and for its intrinsic value as a remnant landform”. This area is a remnant fragment of this glacial period which may have created what appears to be a fragmented distribution of species such as *L. menalcas* (known for its patchy distribution with its range). Second, it was not possible to model the dispersal abilities of the study species, or barriers to dispersal, though these factors are also likely to influence their distributions in the landscape. For example, modelling environmental variables that were thought to explain the restricted distribution of *Hoplogonus simsoni* in NE Tasmania did not predict the presence of this species but suggested that a geological feature at the landscape-scale (i.e. a batholith) may limit the species' dispersal and explain its restricted distribution (Meggs *et al.* 2004). It is possible that during the last Ice Age, the study species may have been excluded from some geographic areas to which they have not been able to return because of barriers to dispersal, such as mountains, rivers and unsuitable dry forest (all of these barriers feature close by or within the study area, particularly river systems of the Arve and Picton).

#### **6.4.4 Implications of the findings of this study for the management of Tasmania's threatened stag beetle.**

The results of this study suggest that all of the study species remain in harvested sites after clearfell burn and sow (CBS) regimes (at least after the first rotation). It

is likely that their persistence on these sites is facilitated by the presence of residual CWD from logging operations (e.g. regenerating forest from 1990s). Whether these logs will support them until the forest is at the stage where it can replenish the site with CWD remains unknown.

For management purposes the models identified in Chapter 5 are thought to be best to predict presence of the study species. These models are thought to be more reliable because they capture more of the characteristics of the CWD that are thought to be important for managing the beetles. Similarly to Chapter 5, the site-scale modelling suggests that *age of regen* and *forest class* are also important for predicting species presence; however, when developing models that use fine scale (e.g. rotten-wood types) and site-scale predictor variables (called CWD-site variables in Chapter 5) the most influential predictor variables in the BRT and BGLM models will almost always be the rotten-wood types. While these fine scale predictor variables are found to be most useful in predicting the probability of the species occurring, the on-ground surveys that are required to collect the fine scale data (identifying a rotten-wood type and the proportion of a rotten-wood type in a log) are intensive and time-consuming, and only offer a ‘snapshot’ of information on the current distributions of species. These surveys cannot reveal whether site or landscape conditions are suitable and sufficient for the long-term persistence of the species. Therefore, a practical management alternative to on-ground surveying is to assume that a suite of species is likely to be present in suitable habitat across the landscape, and to apply management practices that best maintain adequate habitat into the future, while recognising that characteristics of the forest will change after logging.

The current management guidelines for Tasmania’s threatened stag beetle, *Lissotes menalcas*, set under the Biodiversity Values Database (BVD, which provides information on *L. menalcas*’ range and habitat descriptions for use in site assessments when forest activities are planned), are broad and ill-defined. Below is an outline, discussing how these guidelines could be improved by applying some of the knowledge of this species habitat preferences revealed in this study.

The first provision covered in the BVD states that *L. menalcas* is “dependent on a continuing supply of rotting logs on the ground and maintenance of their surrounding microclimate”. The results of this study revealed that certain forest



activities and particular wildfire intervals give rise to conditions that constitute high quality habitat (and a supply of rotting logs) for *L. menalcas*. Specifically, the findings in this chapter suggest that four forest elements present at site-scale increase the likelihood of finding *L. menalcas*: a mature eucalypt element, forest with no mature eucalypt and tall dense middle-age regrowth, young forest regenerating from timber harvesting, and old-growth. All these ecological conditions will act to provide a continuing supply of rotting logs in the landscape, provided they are managed appropriately. For example, it is unlikely that *L. menalcas* will survive in young regenerating forest after clearfell, burn and sow (CBS) if rotation lengths are short (<100 years), since previous research has shown that CBS over short intervals decreases the volume of dead wood over time (Grove *et al.* 2002). However, with careful planning of forestry activities the CBS technique can be applied and still maintain populations of *L. menalcas*, if the silvicultural regeneration that results is managed at the landscape-scale. That is, CBS activities need to be strategically planned throughout the production-forest matrix so that (a) large forest areas do not undergo CBS at the same time, (b) suitable viable habitat remains in the vicinity of CBS operations, and (c) standing and fallen timber is left behind after CBS operations. A recent study by Wardlaw *et al.* (2012) found that “Silvicultural regeneration can recover to eventually have a similar biodiversity as mature forest if remnant mature forest exists within 400 m (or 150 m where a high cover of rainforest plants is important). This remnant mature forest should be provided through the reservation / retention of between 12 and 22% mature eucalypt forest in the surrounding 1 km of landscape”. Such strategic planning of the production-forest matrix can thus provide for the maintenance of biodiversity in Tasmania’s southern wet-eucalypt forests.

Another provision under the BVD states that *L. menalcas* can “survive wildfire and selective logging”. The findings in this chapter suggest that *L. menalcas* may occur more frequently in forests altered by forestry activities such as “middle-aged (30 year old) regenerating forest from partial logging” than in unaltered forests such as old-growth (though not old-growth without a mature eucalypt element). This does not mean that forests subject to natural disturbances such as wildfires are unsuitable for *L. menalcas*. Wildfires contribute to the creation of dead-wood habitat, and the results of this indicate that *L. menalcas* occurs with high probability in wet-eucalypt forests containing regrowth from wildfire.

However, this study found that *L. menalcas* favours a mature *E. regnans* element that tends to arise under certain conditions of low to moderate fire frequency. Therefore, a hot burn and high fire frequency may have negative impacts on the presence of *L. menalcas* because they may reduce volumes of CWD.

The BVD states that *L. menalcas* has been found in “older-age regrowth resulting from logging; however the effects of clearfelling, regeneration burning and plantation establishment are uncertain”. The results of this chapter indicate that the species is able to persist in young plantations most likely as a consequence of legacy CWD remaining from 1990s logging operations. However, this study has also highlighted their continued persistence in these altered landscapes is reliant on three things: the long-term presence of legacy CWD, the length of time until the regenerating forest stand is able to provide CWD to the forest floor and whether the surrounding forest contains suitable habitat to which beetles can disperse.

While the findings of this study can improve current management guidelines for *Lissotes menalcas*, ultimately the best conservation strategy for *L. menalcas* would be to manage entire forests rather than specific beetles, so that the ultimate goal of management is to provide a forest ecosystem that bestows suitable habitat (sufficient logs and sufficient connectivity). This landscape-scale management approach should also be extended to the other five species included in this study. As similar forest elements were found to increase the likelihood of occurrence of all species then the same management principles can be applied to the protection of this entire group. It would be beneficial to construct a map of the habitat requirements at the site-scale and strategically retain mature forests throughout the production-forest matrix bearing in mind that forests are dynamic entities. Managing for mature forests (that generate log habitat) means concurrently managing for young forests and allowing them to mature. If this approach is done at the right spatial scale then it ensures adequate mature trees and adequate up-and-coming mature trees. This strategic approach will ensure that adequate dead-wood resources will always be available to saproxylic beetles in production-forest landscapes.

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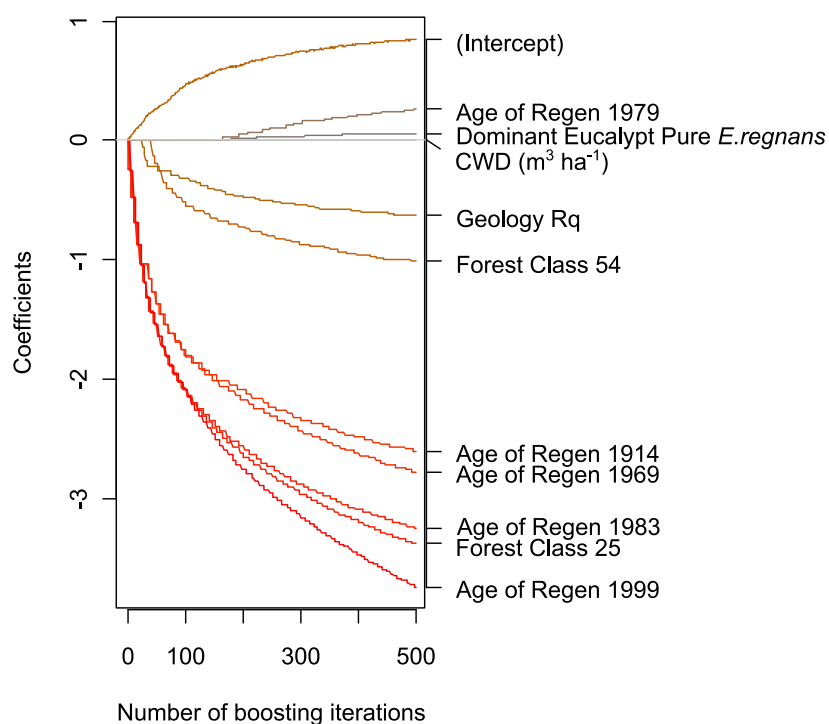
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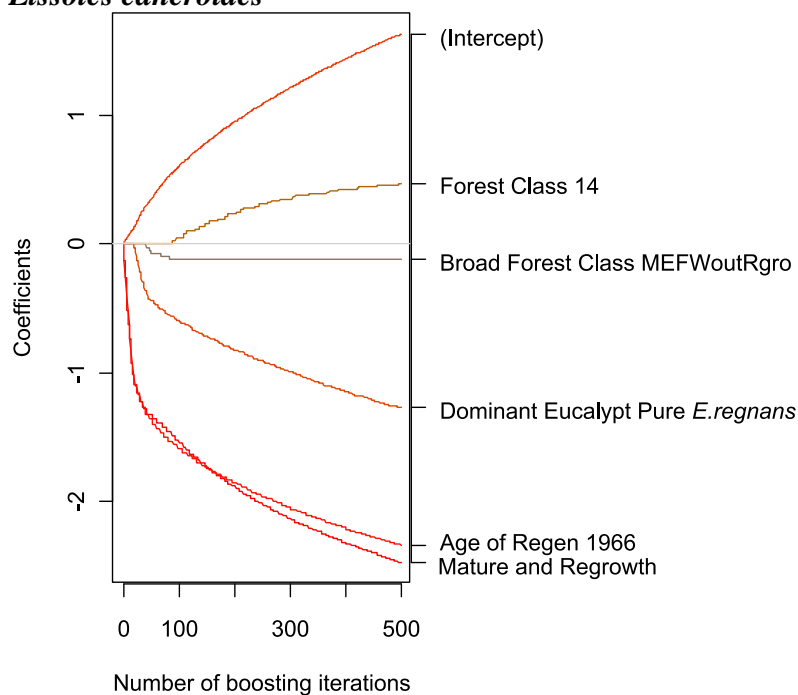
## APPENDIX 6.1 BOOSTED GENERALISED LINEAR MODELLING PLOTS WITH SITE-SCALE PREDICTOR VARIABLES

Relative influence of each predictor variable included in the BGLM model for each species.

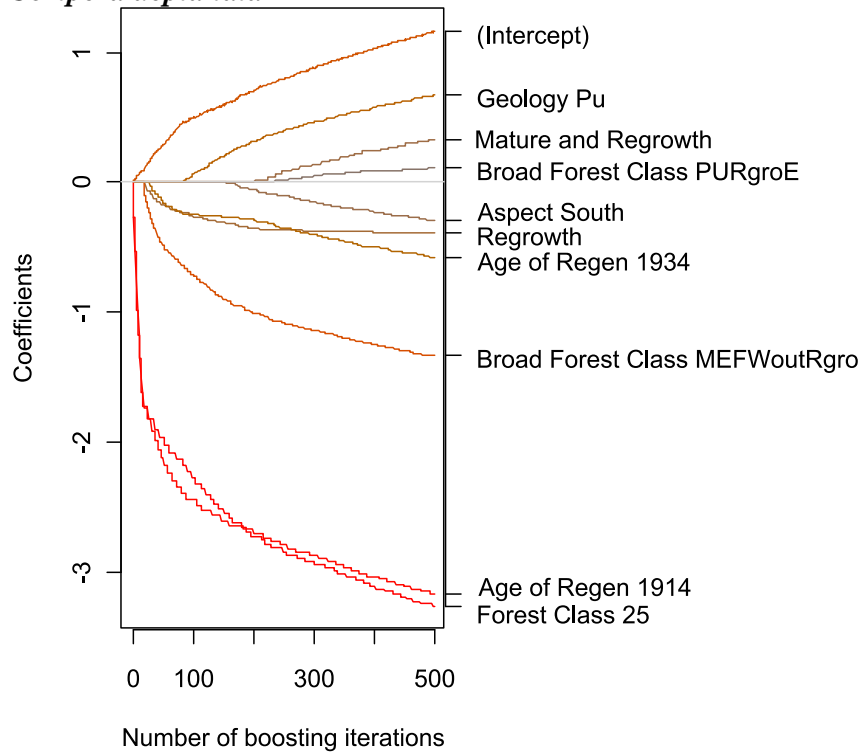
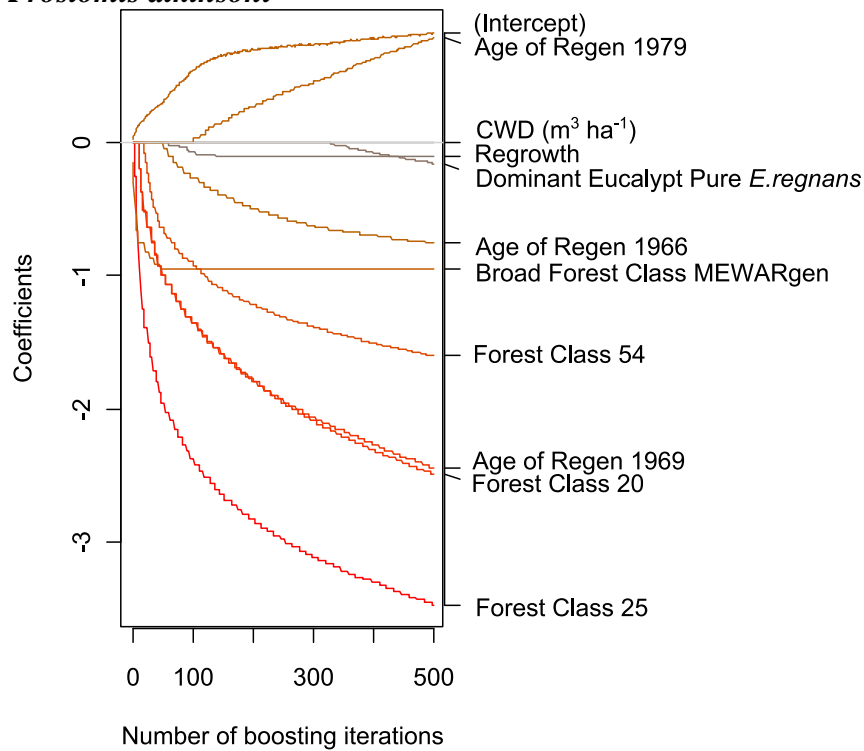
### *Lissotes menalcas*

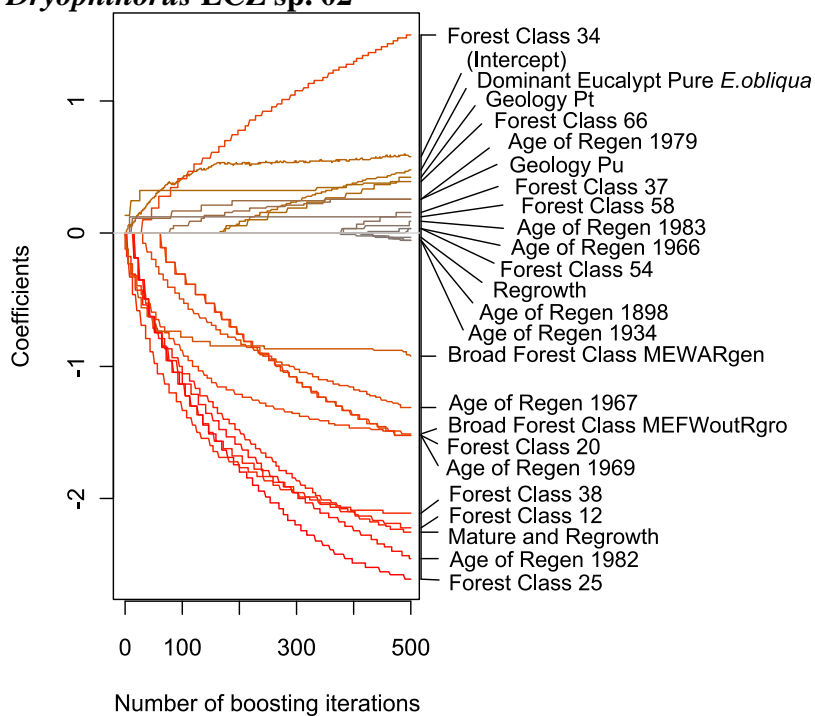
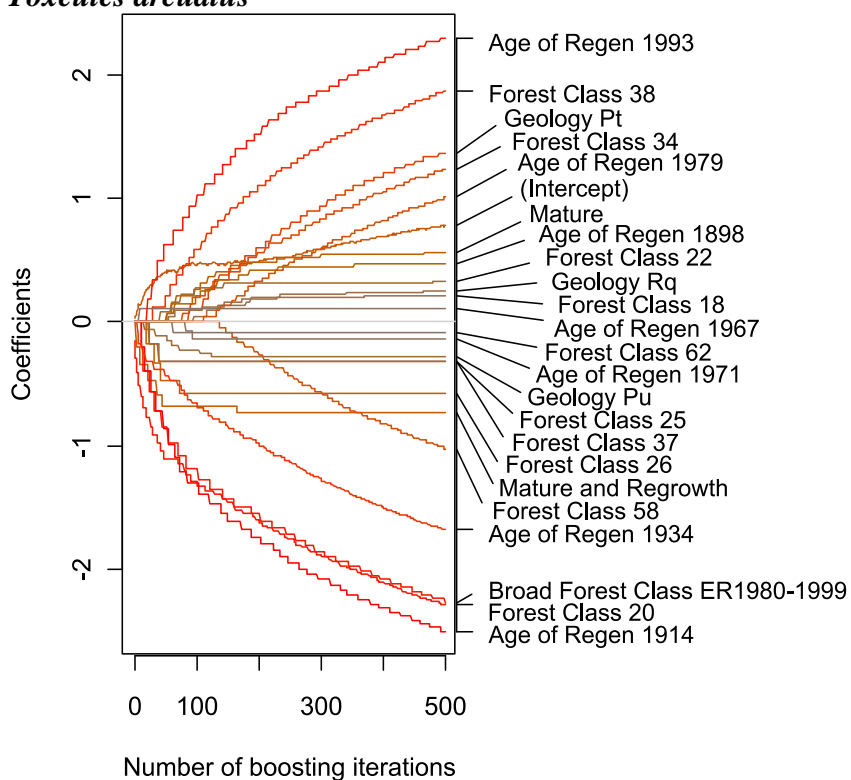


### *Lissotes cancroides*





*Coripera deplanata**Prostomis atkinsoni*

***Dryophthorus* ECZ sp. 02*****Toxentes arcuatus***

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## CHAPTER 7 GENERAL DISCUSSION

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Several key findings of this study further the understanding of saproxylic beetles in production forest in southern Tasmania. It is the first study in Tasmania to use a set of complementary studies to document some life-history attributes, and identify habitat requirements of selected saproxylic beetles by applying predictive habitat models. It provides some important research tools for identifying habitat at varying spatial scales and shows how effective these tools are at identifying important habitat elements at these scales. The life-history studies complement the habitat modelling by identifying some of the strategies employed for living in dead wood and how these affect species persistence in a fragmented landscape.

### 7.1 Habitat requirements of saproxylic beetles at varying spatial scales

This section summarises the habitat each species is thought to require. These summaries demonstrate that the beetles do share some ecological needs, but they have markedly different ones too. It may therefore be unwise to rely on a single management strategy, but instead focus on a multi-species approach. This is achieved by structuring management strategies around the ecological requirements of several species (Lambeck 1997).

#### 7.1.1 *Lissotes menalcas*

Due to its patchy distribution in a restricted range (largely in the production-forest landscape) *L. menalcas* has been listed as a threatened species (Section 2.2.1, Chapter 2). Adults are flightless and movement outside the log is slow. Although they spend most of their life inside the log they are difficult to locate because of their patchy distribution. The species seems to have a preference for *Acacia melanoxylon* and eucalypt logs at intermediate stages of decay (decay class 3-3.5) (Chapter 5). In these logs it has a strong association with dark rotten-wood types of heartwood rot such as ‘mudguts’. However, it also favours dark borer wood and is often found in the frass of *Toxotes arcuatus*, which is associated with dark borer wood (Chapter 5). This cerambycid can perhaps be regarded as an ecosystem engineer (Buse *et al.* 2008) and its activities may alter decaying wood in such a way as to make it more suitable for *L. menalcas* to inhabit.

*Lissotes menalcas* is more likely to be found in shaded dead wood (Chapter 5) and is most prevalent in old forests with a significant non-eucalypt element (Chapter 6). This beetle also favours a mature *E. regnans* element that tends to arise under certain conditions of low to moderate fire frequency (Dick Chuter, pers. comm.). Young to middle-aged stands of regenerating forests (post-clearfell burn and sow) with no mature eucalypt element appear to be particularly unfavourable for *L. menalcas*. *Lissotes menalcas* might be absent in these forests because it may find burnt logs an unsuitable food source (as might the other study species) (Chapter 5). Studies have found that burnt wood is not suitable because fire dries out the cambium; an unfavourable characteristic of dead wood to many saproxylic beetles (Saint-Germain *et al.* 2004).

The patchy distribution of *Lissotes menalcas* may be associated with underlying bedrock (Chapter 6). The species shows an association with wet sclerophyll forests formed on Jurassic dolerite. This bedrock is known to produce fertile soils which produce more productive forests (Harris and Kitchener 2005). In contrast, forests with low-fertility soils derived from sandstone and quartzite are mostly unfavourable (Chapter 6).

Female *Lissotes menalcas*' sexual development appears seasonally cued (Chapter 3). The spermatophore formation in males is seen as early as winter and progresses through to autumn; the females receiving the spermatophore in late spring early summer. Oocytes are present throughout the year but obvious eggs are present in summer (Chapter 3). The clutch size is small with mostly 8 eggs observed. This species is thought to be long-lived taking approximately 2 years to complete its life cycle (Karen Richards and Chris Spencer, unpublished data) which may be dependent on season and nutrition (Chapter 3).

### **7.1.2 *Lissotes cancroides***

*Lissotes cancroides* is common in the southern forests of Tasmania. Adults cannot fly and because they spend most of their time inside rotting wood they are easily located by opening up logs. *Lissotes cancroides* can also be found underneath logs in the warmer months.

*Lissotes cancroides* prefers eucalypt logs at intermediate stages of decay (decay class 3 and 3.5), but can be found in dead wood of many wet sclerophyll and

rainforest species (Chapter 5). The dark rotten-wood types associated with the intermediate decay stages seem to be what makes them appealing to *L. cancroides*; it has a particularly strong association with mudguts, dark borer wood and dark blocky fibrous rot (Chapter 5). This beetle is able to inhabit the drier rotten-wood types, such as dark blocky crumbly rot and dark stringy rot. The drier types of rotten wood may be more readily found on northerly slopes (which tend to have higher insolation than southerly slopes), for which *L. cancroides* has an apparent preference (Chapter 5).

*Lissotes cancroides* is found in forests across a wide range of ages, but is most prevalent in older forests dominated by *E. obliqua*, and eucalypt regeneration arising from minimal disturbance by fire (Chapter 5). It does not favour forests with a rainforest component. The probability of its occurrence increases as volume of suitable dead wood increases.

*Lissotes cancroides* appears to prefer the same habitat as *L. menalcas* and is often found inhabiting the same log. However, the two species are never found co-occurring in close proximity. Competitive exclusion may be one reason for this (i.e. competing for the same resources), but what advantages one *Lissotes* species uses to exclude the other is unknown and was outside the scope of this thesis. Perhaps *L. cancroides* ability to inhabit a wider range of rotten-wood types, decay classes and drier sites has helped it avoid competitive exclusion. Alternatively, when competing for a place inside a rotting log they may use resource partitioning to be able to co-occur by feeding on different rotten-wood types (Chapter 5).

*Lissotes cancroides* sexual development appears to be less constrained by seasonal cues (Chapter 3). The spermatophore formation in males is in early spring and progresses through to autumn; the females receiving the spermatophore in early spring through to the end of summer (Chapter 3). Oocytes are present throughout the year and obvious eggs have been observed in all seasons apart from late autumn/early winter (Chapter 3). The clutch size is slightly larger than *L. menalcas* with mostly 12 eggs observed.

### 7.1.3 *Coripera deplanata*

*Coripera deplanata* is a common species in the southern forests of Tasmania. Adults are flightless but move quickly among the forest-floor debris (pers. obs.).

Only larvae live continuously inside dead wood; emerging adults are not thought not to re-enter the logs (pers. obs.). The species seems to have a preference for eucalypt logs in intermediate stages of decomposition (decay class 3 and 3.5) (Chapter 5). The species has strong associations with many dark rotten-wood types such as dark blocky fibrous rot, mudguts, dark stringy rot and dark borer wood (Chapter 5). The predictive habitat models suggest that it favours sun-exposed sections of logs rather than shaded ones (Chapter 6).

*Coripera deplanata* occurs mostly in dry north-facing forests with young to middle-aged stands of eucalypt regeneration arising from previous clearfelling (Chapter 6). At these sites it may persist through making use of the low volumes of ‘legacy’ dead wood carried over from the preceding stand (Chapter 5 and 6).

#### **7.1.4 *Prostomis atkinsoni***

*Prostomis atkinsoni* is a common species in the southern forests of Tasmania. Adults can fly but this has only been observed during the warmer months. Both larvae and adults are easily located inside suitable dead wood because larvae never leave the log and adults rarely do so.

The species appears to have a preference for eucalypt logs in intermediate stages of decomposition and it has a particularly strong association with a newly characterised rotten-wood type called gingerbread rot (Chapter 5). Experimental evidence suggests that gingerbread rot is a food-source for *P. atkinsoni* (Chapter 4). This type of rotten wood may have its origin in abandoned termite galleries, but is possibly engineered by *P. atkinsoni* as it is thought to compress the rot, giving it a smooth appearance much like gingerbread. However, it may also occur in other rotten-wood types such as dark borer wood, dark stringy rot and mudguts. It is more likely to be found in sun-exposed sections of logs than shaded sections.

*Prostomis atkinsoni* occurs in forests of a wide range of ages, but is most prevalent in older forests and in young to middle-aged stands of eucalypt regeneration arising from past clearfelling (Chapter 5). In the younger regenerating forests it occurs primarily in logs that are a legacy from the pre-clearfell stand. The greater the volume of suitable logs at a site, the higher the probability of occurrence of *P. atkinsoni*. It occurs throughout the study area, but is more predictably present towards the southeast. It shows no obvious association

with any landscape-scale processes such as aspect and geology, perhaps because of its strong association with local-scale factors that are ‘lost’ within the biophysical factors and landscape processes at greater spatial scales (Chapter 6).

#### **7.1.5 *Dryophthorus* ECZ sp. 02**

*Dryophthorus* ECZ sp. 02 is thought to be common in the southern forests of Tasmania, although its cryptic nature makes it difficult to detect in rotting logs. It is a flightless weevil that is rarely seen outside eucalypt dead wood.

This beetle prefers *E. obliqua* logs and appears to inhabit eucalypt logs exclusively, often at intermediate to late stages of decomposition (decay class 3-4) when these logs support large amounts of dark rotten-wood types like mudguts, dark blocky fibrous and gingerbread rot, all of which are highly favoured by this species.

*Dryophthorus* ECZ sp. 02 is prevalent in both old and young forests, including those in which eucalypts are regenerating from both natural fire disturbance and clearfelling (Chapter 5). It’s presence in young regenerating forests is probably because it is able to inhabit dead wood that is a legacy from the previous stand. It is patchily distributed throughout the study area. It is yet to be determined why it has a patchy distribution but it may be due to wildfire (destroying habitat with no close logs to migrate to) or perhaps underlying geology (Chapter 6). For instance, frequency of occurrence of *Dryophthorus* ECZ sp. 02 increases in areas where the underlying bedrock is glaciomarine mudstone and sandstone (Chapter 6). These areas may produce dead-wood habitat that is more suitable for the beetle to inhabit than dead wood derived from forests with different underlying bedrock.

#### **7.1.6 *Toxotes arcuatus***

*Toxotes arcuatus* is commonly found in the southern forests of Tasmania. Adults fly as soon as they emerge from a log (Froggatt 1923) and do not re-enter; therefore, opening up rotting logs is an unreliable way of detecting adults. The larvae may need large areas of decomposing wood in comparison to other saproxylic beetles because they tunnel vigorously, consuming large amounts of rotting wood (Froggatt 1923). The species will readily inhabit eucalypt logs, but may have a preference for dead wood from *Acacia dealbata* (Chapter 5). The presence of *A. dealbata* at sites may indicate the beetle likes sites that have

undergone disturbance. The local dominance of *Acacia dealbata* is a sign of gross past disturbance because areas that are burnt at short intervals will tend to be dominated by *A. dealbata* and *P. apetala* (McCarthy *et al.* 1999).

*Toxeutes arcuatus* appears to have a preference for logs in early stages of decomposition (decay class 1-2), where it is strongly associated with discoloured wood (Chapter 5). A log in early stages of decomposition ensures the log will remain structurally intact, and the larva safe from predators and the elements. The log will therefore be suitable for the beetle to complete its life cycle, which can take up to 11 years (Chapter 2). The species has a particularly strong association with specific pale and dark rotten-wood types. The pale rotten-wood types pale spongy rot and pale stringy rot are often seen in a log at an early stage of decomposition and dark rotten-wood types, such as dark stringy rot and dark borer wood, are found in the early to intermediate ages of decomposition (decay class 3 and 3.5)(Chapter 5).

*Toxeutes arcuatus* occurs throughout the study area in old mixed forest with a mature eucalypt element, but is also prevalent in old to middle-aged stands of eucalypt regenerating from natural fire disturbance after a long fire interval (Chapter 5). As previously stated it appears to like disturbance that provides forests with a local stand of *A. dealbata* but does not like areas that have been significantly affected by fire from clearfelling (CBS) or intense wildfires (Chapter 5). The dynamics of the fire and activity at the site after a clearfell burn may change the characteristics of logs making them unsuitable for oviposition or subsequent survival of larvae. This supposed fire-intolerance has been documented in other saproxylic beetles (Saint-Germain *et al.* 2004) and is therefore a plausible explanation for this species absence at sites that have been intensively managed and/or endured hot fires (Figure 6.3) (e.g. 1967 fire; Dick Chuter, pers. comm.).

## **7.2 An approach using multiple lines of research will help in understanding the management needs of saproxylic beetles**

The research was structured into two different strands that revealed new information about the life-history of these species and their habitat requirements. The overall aim of the study was to produce better research tools for managing these beetle species in production forests by combining the results from the two



lines of study. But the individual studies that make up the project provided some useful insights in their own right and the sub-headings for the paragraphs that follow state the main findings and the research is then discussed.

*Seasonal patterns of sexual development in sympatric species may explain differences in relative abundance*

Seasonal activity and reproductive biology can help identify how a species has adapted its life cycle to the natural forest environment. For example, there is some evidence to suggest that *L. menalcas* and *L. cancroides* are able to coexist in their forest habitat because their reproductive behaviour differs across seasons; female *L. menalcas* sexual development being more seasonally cued than *L. cancroides* (Chapter 3). Understanding reproductive behaviour will bring us closer to understanding the population dynamics of these beetles and provide a picture of their adaptation to the natural forest environment against which the challenges of managing production-forest landscapes can be assessed. One approach to this management would be to model persistence under various natural and anthropogenic disturbances to see how populations respond (e.g. population viability analysis) (Fox *et al.* 2004) a modelling technique which is more likely to produce meaningful outputs when reproductive parameters are included in the model.

The life-history strategies they evolved may disadvantage these beetles by making them vulnerable to localised extinction, particularly when the continuity of log supply is interrupted. Species such as *Dryophthorus* ECZ sp. 02 and *L. menalcas* that are patchily distributed throughout the production-forest matrix may be particularly at risk. However, if in the long-term, forestry intensifies and the elements of habitat described in Section 7.1 decrease then it is possible that the more readily encountered study species will become vulnerable to localised extinction. Accordingly, the future of saproxylic beetles in these managed areas will depend on maintaining an adequate supply and configuration of older, unharvested forests in the production-forest matrix.

*Mycophagy in saproxylic beetles is difficult to establish*

It is still unknown if the study species' are xylophagous or mycophagous; however, *P. atkinsoni* actively ingests wood-rotting fungi, in particular brown wood-rotting fungi (Chapter 4). A brown wood-rotting fungal species isolated from dead wood in Tasmanian wet-eucalypt forest matched the genus *Pleurotus* in

GenBank. Similarly to the example from Japan (Tanahashi *et al.* 2009), the *Pleurotus* from Tasmania was found in decaying wood and ingested by a saproxylic beetle, *Prostomis atkinsoni*. Because the Japanese have found a lucanid species feeding on *Pleurotus* it is feasible that related Tasmanian lucanids, *Lissotes menalcas* and *Lissotes cancroides* may also feed on *Pleurotus*. Further research into the diet of other saproxylic beetles in Tasmania is sure to discover that many feed from the fungi that create rotten wood.

Understanding the diet of these beetles is not only interesting from an ecological standpoint, but also aids in their conservation. If we know what types of rotten wood the beetles prefer to feed on then we can manage for these in forests to ensure they continue to develop in CWD. However, there remains much to do to gain a better understanding of the fungi that form these types of rotten wood and the relationship they have with saproxylic beetles (Komonen *et al.* 2000, Chapter 4). Further information about the mechanical and trophic relationships between these beetles and their assumed fungal food will help us to understand how these species might act as ecosystem engineers, facilitating the breakdown of wood and the release of nutrients, a vital role in forest ecosystems (Wardlaw *et al.* 2009). Ecosystem engineers provide a free service to forest managers; increasing nutrients and promoting soil function, features imperative to tree growth.

#### *Dark rotten-wood types are ecologically important*

At the local scale, dark rotten-wood types are invaluable. The beetles seem to have a predilection for these, especially mudguts, dark borer wood and dark blocky fibrous, a result consistent with other studies on saproxylic beetles (Yee *et al.* 2006; Harrison 2007). These dark rotten-wood types are chiefly, but not exclusively, represented in large eucalypt logs (Yee 2005; Yee *et al.* 2006; Hopkins 2007; Wardlaw *et al.* 2009). However, for the first time in Tasmania we have evidence that rotting logs from non-eucalypt tree species common in wet sclerophyll forests are also suitable habitat for saproxylic beetles, with some species demonstrating a preference for them over eucalypt logs. Non-eucalypt species are generally less common but they can support dark rotten-wood types, suggesting that they also make a valuable contribution to dead wood habitat (Chapter 5).

Dark rotten-wood types are found in the dead wood of many tree species and are ecologically important but their genesis and succession remain unclear. What also remains unclear is the feeding relationship between saproxylic beetles and dark-rotten-wood types. The diet of saproxylic beetles is clearly very complex (Chapter 4) and more work will improve our understanding of the benefits that the beetles derive from feeding on rotten wood, in particular the dark variety.

*Forest structural complexity is important*

The presence of a mature eucalypt element is important because it provides long-term suitable dead wood habitat (Lindenmayer *et al.* 2002).. In addition to this it is the main contributor of large volumes of dead wood and large-diameter logs, along with the associated dark rotten-wood types that many of the study species favour. In combination with a mature eucalypt element, middle-aged regenerating forest arising from wildfire is important (Chapter 5). The middle-aged element will go on to contribute to the dead wood on the forest floor long after the mature element has disappeared, and if fire intervals are long enough it will become the mature eucalypt element. A forest with a mature eucalypt element and a middle-aged element results in a multi-aged stand that can add dead wood to the substrate in the future. These stands add structural complexity to the forest and are important because the attributes they provide, such as trees from multiple aged-cohorts, large trees and large-diameter logs, enhance the creation and diversity of dead wood shown to increase the diversity and abundance of saproxylic species (Déchéne *et al.* 2010; Michel *et al.* 2011).

The qualities these logs possess, in particular those derived from mature eucalypts (diameter, volume and dark rotten-wood types) mean these logs often prevail after wildfire. Wildfire converts mature eucalypt to dead wood and does not always destroy pre-existing rotting logs (Grove and Stamm 2011). This study provides supportive evidence that dead wood inherited from the previous stand is able to support saproxylic beetles (Chapter 5 and Chapter 6). These logs persisting after wildfire disturbance are acting as a “lifeboat” and may be crucial when future dead wood input is questionable and localised extinction a possibility.

*Predictive habitat models can help establish habitat requirements*

Different aspects of a beetles’ relationship with its dead-wood habitat were explored using novel modelling techniques (Chapter 5 and Chapter 6). The information provided by these models led to exploring species presence and

absence based on different aspects of a species' relationship with its environment at varying spatial scales. The various outcomes of these models helped to establish that habitat requirements at the local scale are best at predicting presence of these species (Chapter 5). Landscape features say little about the frequency of occurrence of these species so they cannot be relied upon in drawing conservation plans. Other studies which have set out to determine what ecological processes affect the presence/absence of saproxylic beetles at various spatial scales have also found local-scale environmental factors to be good at predicting incidence. For example, the occurrence of the passalid *Odontotaenis disjunctus* was most dependent on fine-scale environmental factors 'decayed wood' and 'log surface area' in a multi-scaled approach to predict incidence of the species in Louisiana, USA (Jackson *et al.* 2012). Other studies have found that several environmental features are important for managing species at varying spatial scales, and management can begin from the finest scale. For instance, Razgour *et al.* (2011) state that "multi-scale models offer an important tool for identifying conservation requirements at the fine landscape level that can guide national-level conservation management practices".

### **7.3 Saproxylic beetle species are ecologically distinct from each other**

A beetles' presence or absence in a log may depend on factors in addition to the habitat requirements described in Section 7.1. This is evident where a log supports more than one of the study species, indicating that although different species choose the same log; within this log are many ecologically distinct habitats. In this study the different species do not coexist in the same area in the rotting log and a log can be suitable to many of the study species but only one or two are found in the log. This ability to occur inside the same log but not to coexist may be due to resource partitioning, a behaviour that is recognised in other saproxylic species (Déchêne 2010). The beetles may be feeding on different rotten-wood types within the log which may be one reason they occur in the log but never coexist. Species that are associated with the same rotten-wood types may be able to overcome competition for the same resource by feeding at different times or being able to feed on a wider range of resources. Alternatively, the beetles may be experiencing competitive-colonisation, a behaviour that has been observed in other saproxylic beetles, where arrangement of species inhabiting the log is due to

competitive exclusion (Kadowaki *et al.* 2011). Competition and colonisation may be determining the fate of the study species through competition if the dynamics of a patch of habitat is driven by local disturbance. This disturbance then opens up the opportunity for an inferior competitor to colonise habitat, particularly when a dominant competitor is limited in its dispersal or has specialised niche requirements (Kadowaki *et al.* 2011).

## 7.4 Concluding remarks

As a result of this study, we can for the first time be more conclusive regarding the characteristics that generate suitable habitat for some key saproxylic beetles in Tasmania. This study however, is limited for several reasons: the complexities of the ecology of saproxylic beetles, the difficulty in accounting for historical and biophysical factors in the models, the relationship between dead wood and wood-rotting fungi, dispersal capability of the study species and limited understanding of population dynamics. There are still many discoveries to be made about the ecology of saproxylic beetles and further research should include:

- collecting more data on the life-history traits of saproxylic beetles to establish life tables (Chapter 3).
- investigating mycophagy/xylophagy in other saproxylic beetles; particularly the ecosystem engineer *T. arcuatus* as it may play a major role in making dead wood available for many saproxylic species (Chapter 4).
- validating the predictive habitat models through targeted field surveys and refining them accordingly (Chapter 5 and 6).

### 7.4.1 A way forward in our ecological understanding of saproxylic beetles

At present the study species are not responding (in terms of presence/absence) greatly to site-or landscape-scale processes, at least in the study area. Instead, presence can be more accurately predicted using log attributes and the beetles seem to be responding to dead wood suitability at this finer scale. What defines suitable dead wood is determined by the ecological processes working at the local scale to provide rotten-wood types (Chapter 5). At the local scale the beetles' needs are currently being met, but future suitable dead wood habitat may be

reduced in the production-forest matrix (Grove and Stamm 2011). We need to improve our ecological understanding of the relationship saproxylic beetles have with dead wood. This means further research into specific attributes of dead wood, the processes that maintain rotting logs in the landscape and how the beetles respond to these.

Expanding our knowledge of the population ecology of these beetles may show how they coexist and change over time and space. Complementary studies on such population dynamics should include factors that regulate a population. In the case of saproxylic beetles this would mean accounting for density-dependent factors such as predators and food supply, and density-independent factors (such as wildfire and clearfelling).

Persistence in a fragmented landscape of production forest is dependent on successful dispersal (Thomas 2000; Ewers and Didham 2006). Many saproxylic beetles are thought to be poor dispersers (Drag *et al.* 2011), and this is likely to be the case for many saproxylic beetles living in the cool-temperate wet-eucalypt forests of southern Tasmania. If we know how far these beetles are capable of dispersing then we can make informed decisions regarding the spatial arrangement of suitable habitat in the production-forest matrix. To do this we also need to further our ecological understanding of the processes that supply dead wood.

Recent studies have investigated the dynamics of dead wood in Tasmanian wet-eucalypt production forests, modelling the rates of log decay and disturbance dynamics (Stamm 2006, Grove *et al.* 2009; Grove and Stamm 2011). More modelling of dead wood after CBS treatments may help to better understand how to manage dead wood better under the CBS regime. The dead wood created after a clearfell burn is uniform and often removed. In contrast, wildfires rarely burn in the uniform way that is seen after clearfelling and wildfires are not always stand-replacing (Jackson 1968). What is more commonly observed in these forests after wildfire is a matrix of forest burnt at varying degrees dependent on how much fuel is available and moisture levels (Mutch 1970). Often ‘fire-skips’ occur leaving some living and dying trees behind (Turner *et al.* 2009). This study indicates that where dead wood is not destroyed by these fires it is able to continue to provide a suitable habitat for saproxylic beetles.

It is hoped that advances in our understanding of the autecology of saproxylic beetles and the dynamics of dead wood will stimulate the development of tools that make it possible to predict the long-term probability of a species persisting in a given landscape, under different scenarios, whether natural or man-made. One such tool is population viability analysis (PVA), and the more complete the picture we have of beetle autecology and dead-wood ecology the better this type of model will perform, allowing us to more accurately predict the long-term survival of these species under proposed management scenarios and disturbance events like wildfire (Bessinger 2002).

#### **7.4.2 Conservation of saproxylic beetles in the production-forest landscape**

The goal of conserving saproxylic beetles in production forest is to establish management strategies that will provide for their habitat requirements and ensure their persistence (Siitonen 2000). This thesis reaffirms that unharvested forests, their size and their spatial arrangement in the production-forest matrix are central to the management of saproxylic beetles. The retention of late-successional forests in the matrix is really important, but so is maintenance of the natural disturbance regime of these forests. Natural disturbance will continue to provide multi-aged stands and the heterogeneous dead wood habitat that is a product of these stands, something that currently clearfelling is not capable of doing (Wardlaw *et al.* 2012; Lindenmayer *et al.* 2013). This natural disturbance at various spatial and temporal scales leads to the spatial arrangement and continuous supply of suitable logs over time. The spatio-temporal arrangement of habitat means that the beetle moving around the forest should be able to locate a suitable rotting log when they require them.

With clearfelling (under the CBS regime) lots of logs are created initially, but the volume of pre-existing and newly formed woody debris is reduced over time through the application of a post-harvest regeneration burn (Grove and Meggs 2003). However, modelling dead-wood dynamics after wildfire has demonstrated volumes are better maintained than after a regeneration burn and continuation of dead wood occurs if the return interval of wildfire is less than 300 years and more than 100 years (Grove and Stamm 2011). Current modelling of the downed wood under the CBS scenario suggests that CBS cycles produce lower volumes of dead wood than wildfire and that the reduction of dead wood continues during the

course of a CBS cycle, probably due to the eventual loss of legacy dead wood (Grove and Stamm 2011). This has several implications for the persistence of saproxylic beetles. This thesis has found that legacy dead wood supports saproxylic beetles in what would otherwise be unfavourable habitat (young silvicultural regeneration). These biological legacies or ‘lifeboats’ may act as a thread of continuity in the production-forest matrix; a lifeline for species that would otherwise disappear from a disturbed site (Franklin *et al.* 2001). Under the CBS regime elements of dead wood are likely to disappear. This includes elements that illustrate heterogeneity of dead wood substrate, such as age, size and decay class (all becoming more uniform). Specific elements favoured by the selected saproxylic beetles established in this thesis, such as dark rotten-wood types, dead wood derived from non-eucalypt tree species and a mature eucalypt component are also likely to diminish under current CBS regimes.

In Tasmania, forestry employs a number of ways of retaining habitat in the production-forest matrix to mitigate the effects of land fragmentation on wildlife. For example, retention silviculture such as aggregated retention ensures pre-harvest forest structure and habitat is retained during harvest (Baker and Read 2011). Various provisions of the Forest Practices Code (2000) require retention of habitat for soil and water conservation and protecting threatened species, while other non-mandatory retention includes the establishment of informal reserves on unworkable terrain (i.e. steep or marshy ground). Large-scale habitat retention in the form of biodiversity corridors have been shown to be valuable for the conservation of wildlife in production forest (MacDonald 2003), including beetles if corridors adequately represent native forest in a region at various spatial scales (Grove and Yaxley 2005). These corridors are an important part of applied conservation in production forests because they ensure better habitat connectivity. However, for effective management of saproxylic beetles they should be used in conjunction with many types of retention or active management.

There are ways which are currently a part of forestry activities that could assist in managing saproxylic beetles in production forests. Grove and Meggs (2003) state that ‘in Tasmania’s wet-eucalypt forest, where wildfire is the main large-scale disturbance, the use of clearfelling followed by regeneration burning (CBS) may currently be allowing the survival of species that in the long-term would be disadvantaged by the ‘benign neglect’ approach adopted in adjacent conservation



areas”. However, if we are to use the CBS technique to actively manage for saproxylic beetles then longer rotations will be needed to provide structural complexity (Franklin *et al.* 2000; Yee 2005 ) and fire suppression or fire intensity trialled at the local-scale (Grove and Meggs 2003).

Planning of coupes in production-forest landscape is also important. If the coupe arrangement in production-forest matrix is carefully planned to minimise large areas of intensively managed forests (including native forest) is interspersed throughout, then saproxylic beetles may have a better chance of locating suitable logs in neighbouring forests. But what of this forest? Should forestry be actively managing this also or leaving it? Benign neglect may not be seen in this case as the optimal management technique because over-mature forests are not able to continually provide suitable dead wood. This study demonstrates that the presence of mature eucalypt is an element looked favourably upon when managing for the selected saproxylic beetles. However, this mature timber habitat is not everlasting and will eventually disappear as rainforest species take over if wildfire intervals are long enough (i.e. over 300 years). In addition, modelling suggests that wildfire intervals of 300 years or more see a reduction in dead wood habitat (Grove and Stamm 2011) and long-term fire suppression is known to change the structural form of the forest (Jackson 1968). Because fire is an important component of the ecological processes in wet-eucalypt forest and largely determines structure and floristics, fire frequency and time since fire should come under consideration when thinking about ways to actively manage reserves in production-forest matrix.

Formal and informal forest reserves, maintain elements of pre-harvest habitat in a harvested area (Franklin *et al.* 1997) but the effectiveness of these reserves relies on preserving native habitat at varying spatial scales within a region (Baker *et al.* 2009). Aggregated retention may be the key to maintaining these elements in production-forest matrix. It would give saproxylic species an advantage in the matrix by retaining a broad variety of tree species, sizes and conditions (Franklin *et al.* 2000). Aggregated retention has previously been shown to retain beetle abundance in the same forests as this study (Baker *et al.* 2009). Careful planning of aggregated retention across the production-forest matrix to maintain the habitat identified in Section 7.1 would give the species featured in this study a good chance of persisting. In addition to using aggregated retention to conserve these

species, studies that identify dispersal rates and distances of saproxylic beetles will aid in planning the spatial arrangement of aggregated retention in production forest.

Where dead wood under the CBS regime is not destroyed it may be harvested for biomass energy production (known as fuelwood). This harvesting of fuelwood, whether by means of firewood for household or industrial use, needs to be controlled and dead wood needs to be recognised as a critical habitat for many organisms and an important part of nutrient recycling that keeps forests healthy.

#### **7.4.3 Conserving saproxylic beetles supports forest biodiversity and health**

This study emphasises the specialised relationships saproxylic beetles have with their habitat, but this relationship is not just about the beetles and dead wood. The beetles play an active role in decomposing wood; as they feed and move around inside the wood they are gradually breaking it down and releasing nutrients as the log decomposes, an activity that is crucial for nutrient recycling in the forest ecosystem (Samuelsson *et al.* 1994; Cobb *et al.* 2010). Their contribution to this process is not only directly through their feeding but also as they tunnel through the woody matrix, distributing fungal spores, allowing gas exchange through the material and providing access for other species. By providing the nutrients and changes to physical and structural attributes of the log so it is accessible to other saproxylic organisms including fungi and plants, saproxylic beetles have the potential to increase biodiversity. Saproxylic beetles are therefore a crucial component to the forest floor community and an integral connection to maintaining biodiversity and the health of the forest as a whole (Jacobs *et al.* 2007).

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