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**Ecology and conservation of ground-dwelling beetles in
managed wet eucalypt forest: edge and riparian effects**

Susan C Baker BFSc, BSc (Hons)

Submitted in fulfilment of the requirements for the degree of Doctor of Philosophy,

School of Zoology, University of Tasmania, November 2006

Declarations

Statement of originality

This thesis contains no material that has been accepted for a degree or diploma by the University or any other institution, except by background information and duly acknowledged in the thesis. To the best of my knowledge and belief, this thesis contains no material previously published or written by another person, except where due acknowledgement is made in the text.

Susan Claire Baker

Statement of authority of access

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Susan Claire Baker

Abstract

Limited understanding of the ecology of ground-dwelling invertebrates in Tasmania has hampered our ability to assess the adequacy of forest management. This thesis documents the distributions of ground-dwelling beetle assemblages in managed, wet eucalypt forests of southern Tasmania, and explores the response of beetles to ecological gradients caused by riparian influences near small streams (since retained riparian corridors are a major conservation tool), and edge effects from recently clearfelled logging coupes. Extensive pitfall trapping using replicated transects at four sites was employed to compare the beetle fauna between five habitats: young logging regeneration, the interior of upslope mature forest, the riparian-upslope transition in mature forest interior, and across coupe edges (both into upslope mature forest and into streamside reserves). Data screening ensured that the primary transect design, which employed traps positioned at unequal distances within transects, was unlikely to produce patterning in beetle distributions attributable to spatial autocorrelation or pitfall trap depletion.

Beetles responded to riparian influences, showing subtle shifts in assemblage composition, and generally reduced abundance or species richness nearer to streams. However, site differences outweighed riparian effects. Beetles assemblage composition differed substantially between young logging regeneration and mature forest: several species were identified as indicators of each habitat. Beetles responded more strongly to edge effects than to riparian influences. Depth of edge influence extended ~ 22 m into unlogged non-riparian forest, but further into streamside reserve edges (up to ~ 65 m). Four beetle species, *Choleva* TFIC sp 01 (Leiodidae), *Decilaus nigronotatus*, *D. lateralis* and *D. striatus* (all Curculionidae), were indicators of mature forest interior.

A second survey compared beetles between logging regeneration, upslope mature forest interior, mature forest interior riparian areas, and streamside reserves that had been logged on both sides, in five stands of each of the four habitats. Streamside reserves (average width 40 ± 6 m ($\pm 95\%$ CI) from reserve edge to stream) supported different beetle assemblages to unlogged areas, and were probably entirely edge-effected.

These results suggest that current corridor provisions, which rely heavily on riparian reserves, may be inadequate to conserve beetles dependent on mature forest interior. Reserve corridors may need to be wider, and should more often be positioned upslope away from riparian areas. Alternatively, a mix of different types of reservation strategies (e.g. conserving some contiguous blocks of mature forest in lieu of widened corridors) needs to be developed to increase the probability that edge-sensitive and mature forest specialist taxa will be conserved.

Acknowledgements

Many people and organisations have supported this research, and acknowledgements are given at the end of each chapter. I received a University of Tasmania Postgraduate Scholarship, and a top-up scholarship from the CRC for Sustainable Production Forestry. To supplement funding from The University of Tasmania, fieldwork was supported by the following grants: a Forestry Tasmania Warra LTER Small Projects Grant, a DPIWE World Heritage Area Grant, and a Maxwell Ralph Jacobs Fund Grant. Funding from Forestry Tasmania provided a scholarship extension to sort and identify beetles collected in the second field trial. FWPRDC and the Geography Student's Society provided travel grants to attend international conferences.

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Contents

Declarations	2
Statement of originality	2
Statement of authority of access.....	2
Abstract	3
Acknowledgements	5
Contents.....	8
Chapter 1.....	11
General introduction.....	11
Background	11
General Research Objectives.....	17
Overview of how the general objectives were addressed.....	19
Presentation of the thesis	21
Statement of co-authorship.....	25
References	25
Chapter 2.....	32
Evaluating spatial autocorrelation and depletion in pitfall-trap studies of environmental gradients	32
Abstract	33
Introduction	34
Methods	36
Results and Discussion.....	39
Acknowledgements	44
References	44
Chapter 3.....	48
Site effects outweigh riparian influences on ground-dwelling beetles adjacent to first order streams in wet eucalypt forest	48
Abstract	49
Introduction	50
Methods	52
Results	58
Discussion	67
Conclusions	71
Acknowledgements	71
References	72
Chapter 4.....	80
Why conservation reserves should not always be concentrated in riparian areas: a study of ground-dwelling beetles in wet eucalypt forest	80
Abstract	81
Introduction	82
Methods	86
Results	93
Discussion	101
Acknowledgements	109
References	110

Chapter 5.....	121
A comparison of litter beetle assemblages (Coleoptera) in mature and recently clearfelled <i>Eucalyptus obliqua</i> forest.....	121
Abstract	122
Introduction	123
Materials and Methods	124
Results	129
Discussion	136
Acknowledgements	140
References	140
Chapter 6.....	145
Estimating edge effects on ground-dwelling beetles at clearfelled non-riparian stand edges in Tasmanian wet eucalypt forest.....	145
Abstract	146
Introduction	147
Methods	150
Results	156
Discussion	163
Acknowledgements	169
References	170
Chapter 7.....	179
Response of ground-dwelling beetles across logging coupe edges into riparian buffers.....	179
Abstract	180
Introduction	181
Methods	183
Results	190
Discussion	196
Acknowledgements	201
References	201
Chapter 8.....	207
A comparison of ground-dwelling beetle assemblages in streamside reserves with those in unlogged wet eucalypt forest	207
Abstract	208
Introduction	209
Methods	211
Results	216
Discussion	223
Conclusion.....	228
Acknowledgements	229
Literature cited	229

Chapter 9.....	234
General Discussion: An overview of factors influencing ground-dwelling beetle distributions in production wet eucalypt forest and their relevance to reserve design	234
Abstract	235
Introduction	236
Ecological patterning of ground-dwelling beetles in wet eucalypt forest	237
Reservation strategies for beetle conservation	247
Directions for future research	254
Conclusions	259
References	260
Appendix 1	271
Pilot study.....	271
Aims	271
Methods	271
Results	272
Conclusions	273
Appendix 2	278
Allocation of sampling effort in Trial 2	278
Aims	278
Methods	278
Results	279
Conclusions	282
References	282
Appendix 3	283
Extra riparian analyses.....	283
Indicator species analysis of beetles in riparian compared to upslope habitat	283
Soil moisture content in riparian-upslope transects	286
References	287
Appendix 4	288
Seasonality of edge response in riparian transects.....	288
Aim.....	288
Methods	288
Results	289
Conclusions	289
References	291
Appendix 5	292
Association of common brown froglets, <i>Crinia signifera</i>, with clearcut forest edges in Tasmania, Australia	292
Abstract	293
Introduction	294
Methods	296
Results	299
Discussion	301
Acknowledgments	305
References	306

Chapter 1

General introduction

Background

Balancing conservation of biodiversity with timber production is a key challenge of modern native forest management. Biodiversity conservation in Tasmanian State Forest is a requirement under State and Federal legislation (Forestry Tasmania 2004), and international agreements such as the Montreal Protocol (Secretariat of the Convention on Biological Diversity 2005). At the same time, meeting long-term timber supply agreements requires the harvesting of substantial areas annually from the commercially important native wet eucalypt forests (Forestry Tasmania 2004, 2005).

The leaf litter layer is a biodiverse habitat within forest ecosystems, supporting a wide variety of invertebrate taxa (Neumann & Tolhurst 1991; Collett 1999). Beetles represent a substantial proportion of the ground-dwelling invertebrate fauna in terms of numbers of both individuals and species (Collett 1999; Baker et al. 2004); and are therefore an important component of native forest biodiversity. For example, 630 species of beetles from 70 families have been recorded from the Warra LTER site in southern Tasmania (www.warra.com). Ground-dwelling beetles are known to be sensitive to forest management practices, both in Tasmania and worldwide (Michaels & McQuillan 1995; Niemelä 1997; Werner & Raffa 2000; Buddle et al. 2006). The abundance, diversity and sensitivity of adult beetles suggests their suitability to represent ground-dwelling invertebrates in assessing the impacts of forest management.

Although substantial areas of tall wet eucalypt forest are protected in national

parks and other reserves (Forestry Tasmania 2004), many invertebrate species may not be well protected by the existing reserve system (Meggs & Munks 2003), and forestry activities are considered a threatening process for some beetle species listed under Tasmanian threatened species legislation (Bryant & Jackson 1999). High community turnover (Baker et al. 2004; Grove & Yaxley 2005) and localized distributions for some species means that ensuring regional persistence of beetle species in areas managed for timber production is important. The extent to which beetles can use, or disperse through, a matrix of logging regeneration, as well as their use of reserve areas within the logging matrix for habitat and dispersal, will affect the metapopulation dynamics and population persistence of beetles in areas subject to timber harvesting (Lindenmayer & Franklin 2002; Ewers & Didham 2006).

Since the 1960s, clearfelling followed by high intensity regeneration burning (clearfell, burn, and sow) has been the standard silvicultural practice used in wet eucalypt forest (Forestry Tasmania 1998). These practices have attempted to mimic the ecological effects of the natural wildfire disturbance regime (Gilbert 1959; Florence 1989; Attiwill 1994), and, although previous clearfelling appears not to have severely impacted beetle assemblages at the stand level, landscape-level impacts including fragmentation and loss of old-growth habitat may have negative consequences for biodiversity including ground-dwelling beetles (Baker et al. 2004). In the future, aggregated retention silviculture where clumps of trees are retained within coupes will be the primary harvesting system used in old-growth wet eucalypt forest (Forestry Tasmania 2005).

The Tasmanian *Forest Practices Code* (Forest Practices Board 2000) and associated legislation are the chief means by which harvesting is regulated to incorporate the conservation of biodiversity and other non-timber values. The *Forest Practices Code* prescribes two types of reserve corridors: streamside reserves and

wildlife habitat strips. Tasmania employs a variable-width stream buffering system (Forest Practices Board 2000). Streamside reserves of uncut forest are a requirement for all streams in catchments exceeding 50 ha, while 10 m machinery exclusion zones are required in smaller catchments. Buffers of at least 20 m (horizontal) width from the watercourse bank to the reserve edge are required in catchments from 50-100 ha, 30 m buffers are required in catchments exceeding 100 ha, and 40 m buffers for rivers and lakes. The primary function of streamside reserves is the protection of aquatic values, although as part of the terrestrial reserve system they also play a role in terrestrial habitat conservation. The *Forest Practices Code* also requires wildlife habitat strips for maintenance of terrestrial habitat. Wildlife habitat strips are 100 m wide strips of uncut forest located every 3-5 km. These are largely positioned as widened streamside reserves, although links up slopes and across ridges to join adjacent catchments are recommended (Forest Practices Board 2000). Reserve corridors (streamside reserves and wildlife habitat strips) have the potential to both preserve mature forest habitat for ground-dwelling beetles, and provide landscape connectivity to facilitate the dispersal of mature forest species that may be unable to use areas of younger forest regenerated following harvesting.

Currently, little is known about the ecology of ground-dwelling beetles in Tasmanian forests. Incomplete taxonomy means that in many cases identification to species is not possible, and little or nothing is usually known of species' habitat requirements, dispersal abilities or sensitivity to anthropogenic change. Nevertheless, Tasmanian ground-dwelling beetles are responsive indicators of local habitat conditions and impacts of forest management, and an important contributor to native forest biodiversity and function, and thus worthy of conservation (Lawrence & Britton 1994; Michaels & McQuillan 1995; Michaels 1999; Baker et al. 2004; Grove & Yaxley 2005). Although many studies have focused on carabid beetles, studying

all ground-dwelling beetle species encompasses a greater variety of habitat and food requirements, trophic levels and dispersal abilities (Lawrence & Britton 1994). Thus the value of all ground-dwelling coleopterans as indicators of the impact of forest management may exceed that of carabids alone.

Forest beetles are potentially responsive to various ecological gradients, and this thesis explores both natural riparian gradients, and human-induced edge effects from logging coupes. Riparian zone boundaries can be difficult to delineate precisely (Naiman & Décamps 1997), especially in wetter ecosystems such as Tasmanian wet eucalypt forest which generally lack distinct strips of riparian vegetation near streams. It is not known whether any terrestrial beetle species in Tasmania depend on riparian areas. However, this is likely given that there are riparian-associated beetles elsewhere (Spence 1979; French & Elliott 1999) and that other invertebrates, such as terrestrial amphipods, have distributions that vary with distance from streams (Richardson & Devitt 1984).

The abundance and species richness of animals is generally thought to be higher in riparian than in upland habitats (Stauffer & Best 1980; Doyle 1990; Catterall 1993) although this is not always the case, and some species may prefer upslope areas (Sabo et al. 2005). The response of ground-dwelling beetles to riparian-upslope transitions has rarely been investigated, although some studies have found beetles to be more numerous and diverse in riparian than upslope areas in forest habitats with ≥ 1000 mm annual rainfall (Brenner 2000; Catterall et al. 2001; Davis et al. 2001; Hutchens & Wallace 2002). Brenner (2000) found differing ground-dwelling beetle community composition and greater species richness in riparian than upslope areas in wet coniferous forest in Oregon, a vegetation type analogous to the wet eucalypt forest studied here.

Edge effects commonly arise near the boundaries between adjacent habitat

patches, leading to a variety of ecological changes (Peltonen et al. 1997; Ries et al. 2004). Clearfelling is a major source of abrupt edges between logging coupes and adjacent unlogged mature forest. Both abiotic (e.g. microclimate) and biotic (e.g. abundance and distribution of species, species behaviour and interactions, vegetation structure) changes have been recorded at clearfelled logging coupe edges (e.g. Helle & Muona 1985; Chen et al. 1995; Peltonen et al. 1997; Van Wilgenburg et al. 2001). The distance that different types of edge effects penetrate varies greatly, ranging from no effect to influence over several kilometres (Laurance 2000; Ries et al. 2004). However, most studies have found edge effects to disappear within the first 100 m (Murcia 1995; Ries et al. 2004). In managed forest landscapes composed of relatively small coupes of different stand age, the degree of fragmentation, and consequently the total amount of edges between different habitats is increased substantially (Michaels & McQuillan 1995; Peltonen et al. 1997). Forest ground-dwelling beetles have been demonstrated to be sensitive to edge effects elsewhere (Helle & Muona 1985; Magura & Tóthmérész 1997; e.g. Davies & Margules 1998; Didham et al. 1998), and in damp sclerophyll forest in northeast Tasmania (Grove & Yaxley 2005). Didham (1997) documented edge penetration of approximately 100 m for terrestrial invertebrates in Amazonian forest, and noted that this was a much greater distance than for microclimatic factors, suggesting that invertebrates may be particularly sensitive to habitat modification. Westphalen (2003) documented edge effects for vegetation and microclimate at clearfelled logging coupe edges in Tasmanian wet eucalypt forest. He estimated depth of edge influence was 10 m into unlogged mature forest for vegetation, temperature and vapour pressure deficit, and up to 50 m for photosynthetically active radiation. However, until now, the edge responses of animals in this habitat have not been investigated, although the assemblage composition of wet forest ground-dwelling beetles do differ with stand

ages after harvesting (Michaels & McQuillan 1995; Michaels 1999; Michaels & Bornemissza 1999). The existence of edge effects and other consequences of fragmentation (Ewers & Didham 2006) are therefore likely for beetles in Tasmania's managed forests.

Within an ecological community the response of different species to habitat edges varies. Some species may benefit from the changed habitat conditions at edges, generalist species may remain unaffected, while the suitability for forest interior specialist species may be reduced or rendered unusable (Peltonen et al. 1997; Didham et al. 1998). Interacting effects can also influence the degree of edge influence, e.g. edge orientation, other habitat fragmentation effects, edge contrast and temporal changes (Ries et al. 2004); however, edge effects at riparian and non-riparian habitats have rarely been distinguished.

Corridors may be especially sensitive to edge effects, and in some cases may contain no interior habitat (Soulé & Gilpin 1991; Hobbs 1992; Niemelä 2001). There is some evidence to suggest that Tasmanian ground-dwelling beetles may be disadvantaged in retained reserve corridors in forestry areas (Grove 2004; Grove & Yaxley 2005). Further, riparian corridors may be subject to the interacting effects of both edge and riparian influences, the ecological outcome of which is unknown. Since small streams are common in wet eucalypt forest, streamside reserves are a significant component of the terrestrial reserve network. Additionally, since wildlife habitat strips are usually aligned as wide streamside reserves, the reserve corridor network potentially has a strong bias to riparian compared to upslope habitat, although the width of the riparian zone will influence the extent of this bias. By quantifying habitat preferences and the response of ground-dwelling beetles to riparian and edge gradients, it is hoped that this study will provide information to

better inform decisions about the width and positioning of reserve corridors in wet forest landscapes subject to harvesting.

General Research Objectives

The investigations in this thesis were designed with the overall objective of assessing the effectiveness of the width and landscape positioning (riparian versus upslope) of the current reserve corridor prescriptions for providing ground-dwelling beetle habitat in wet forest logging areas in southern Tasmania. The studies undertaken aimed to address these issues by investigating relevant factors affecting beetle distributions. This landscape type was chosen because it is the dominant managed, native forestry system in temperate Australia, and the adequacy of prescriptions for reserves and other habitat retention measures remain largely uninvestigated for invertebrates. The terms ‘ground-dwelling’ or ‘litter’ beetles are used for descriptive value, but it is recognised that pitfall trapping will not necessarily collect all beetle species inhabiting the leaf litter, and will also collect some species with affinities for other habitats (e.g. the soil surface, or canopy-dwellers that pupate or overwinter in the soil or leaf litter). The terms ‘epigaeic’ or ‘ground-active’ could also be applied to the beetles in these studies.

Pitfall trap studies were used to investigate the response of beetles to forest age, spatial influences, riparian-upslope transitions, and edge effects from recently clearfelled and regenerated logging coupes. One goal was to identify any differential responses by beetles at riparian and upslope coupe edges resulting from the interacting influences of edge and riparian effects. From these results, I hoped to determine the distances over which edge and riparian effects influence beetle assemblages, and thereby assess the effectiveness of current corridor widths. Documenting beetles’ riparian response, including assessing their interactions with

edge effects, also relates to evaluating the relative habitat value of riparian and upslope habitats for ground-dwelling beetles in the context of the current bias towards riparian positioning of reserve corridors.

As a consequence of these studies, this thesis also aims to identify indicator species that are sensitive to these processes, to serve as a resource for future studies of beetles in this ecosystem, and provide the basis for future attempts at biological monitoring.

To complement these indirect approaches to assessing reserve effectiveness, a second study was conducted with the aim of directly evaluating whether existing streamside reserves that had been logged on both sides were of equivalent habitat value to continuous forest for ground-dwelling beetles.

In summary, the general research objectives were to:

1. explore the effect of spatial scale on beetle distributions (Chapters 2, 3 and 5);
2. investigate the response of ground-dwelling beetles to riparian influences alongside small streams (Chapters 3 and 4);
3. compare beetle assemblages in young logging regeneration to mature unlogged forest (Chapter 5);
4. document the response of beetles to edge effects at both non-riparian and streamside reserve coupe edges (Chapters 6 and 7);
5. assess the value of streamside reserves and wildlife habitat strips for conservation of ground-dwelling beetles in wet eucalypt forest (Chapters 4, 6, 7 and 8).

The detailed hypotheses and aims for each of these general objectives are given in the introductions of each of the relevant chapters, as cross-referenced above.

Overview of how the general objectives were addressed

The general objectives of the thesis were addressed through two surveys or field trials (hereafter referred to as “Trial 1” and “Trial 2”). Both trials were conducted in Geeveston District State Forest managed by Forestry Tasmania.

Trial 1 was the primary research trial that forms the basis for this thesis. Trial 1 addressed several related research topics concurrently (Chapters 2–7) with a study design that enabled direct comparison of beetle assemblages in the various sampled habitats. Trial 1 employed three one-month trapping periods, spaced every four months between June 2001 and March 2002. This sampling approach provided information about the seasonality of beetles without inflating the number of specimens requiring identification to unrealistic levels. The trial was conducted at four study areas (Warra, Manuka, Picton and Kermandie, Figure 1). Unlogged riparian areas were adjacent to King Creek (Warra), Isabel Creek (Picton), Leas Creek (Manuka) and Critter Creek (Kermandie). Each study area was focused around a recently clearfelled and regenerated logging coupe, and in adjacent unlogged mature upslope and riparian areas. Within each study area, three replicate transects of pitfall traps were located in each of the following habitats (Figure 2):

1. regeneration forest/logging coupe interior
2. mature forest interior – non-riparian
3. mature forest interior – riparian
4. across non-riparian coupe edges
5. across streamside reserve (riparian) coupe edges

Trial 1 assessed the response of beetles to the riparian-upslope transition (Chapters 3 and 4), and to edge effects into both non-riparian unlogged forest (Chapter 6) and into streamside reserves (Chapter 7). This dataset was also used to

compare beetle assemblages in young logging regeneration to mature unlogged forest (Chapter 5), and to check whether the transect layout (unequal distances between traps in transects) was causing pitfall trap depletion or spatial autocorrelation (Chapter 2). Bycatch data for the frog *Crinia signifera* was also explored to assess the edge response of this species (Appendix 5). Further details of the sampling methods are provided in each individual chapter as relevant. Despite considerable effort in searching, the four study areas used were the only sites available that met the requirement criteria for the five habitat types. The Warra and Manuka study areas were located within the Warra LTER.

Trial 2 was a case study of the effectiveness of streamside reserves in the Picton River valley (Chapter 8). Its objective was to assess whether beetle assemblages in streamside reserves that had been logged on both sides were equivalent to those in unlogged areas, or whether habitat value was compromised because of edge effects. Sampling of beetles was conducted in four habitats:

1. streamside reserves with clearfelled logging regeneration either side
2. regeneration forest/logging coupe interior
3. mature forest interior – non-riparian
4. mature forest interior – riparian

Three transects of pitfall traps were located in five replicates of each habitat type (Figure 3). Concentration of previous clearfell logging to the west of the Picton River meant that all streamside reserve and regeneration sites were located there, while three of five unlogged riparian and upslope sites were located east of the Picton River. Beetle sampling was conducted in a single one-month trapping period in October-November 2002.

All beetles collected in both Trials 1 and 2 were identified to family and morphospecies. Since taxonomic knowledge of Tasmanian ground-dwelling

Coleoptera is incomplete, it would not have been possible to identify all beetles to species. Where possible, efforts were made to identify to species the commonly collected morphospecies that are referred to in the thesis chapters. Species identifications were not made for many of the rarer morphospecies.

Presentation of the thesis

The thesis is presented as a series of manuscripts that have either been submitted, or will shortly be submitted for publication. The later chapters refer to earlier chapters for background, and will be submitted for publication once these have been published. The formatting and style varies between chapters, depending on the requirements of individual journals. Because Chapters 2-9 were prepared as scientific manuscripts, some repetition, particularly in the Methods and References sections, was unavoidable. Background information arising from this thesis is referred to by chapter number. Details of authors, publication status, and the journals for which the manuscripts are formatted are provided at the beginning of each chapter.

Figure 1. Location of the Trial 1 study area in southern Tasmania, showing the four study areas Warra, Manuka, Picton and Kermadie. The approximate locations of each habitat type are illustrated. Map prepared by Peter Ladaniwskyj from Forestry Tasmania.

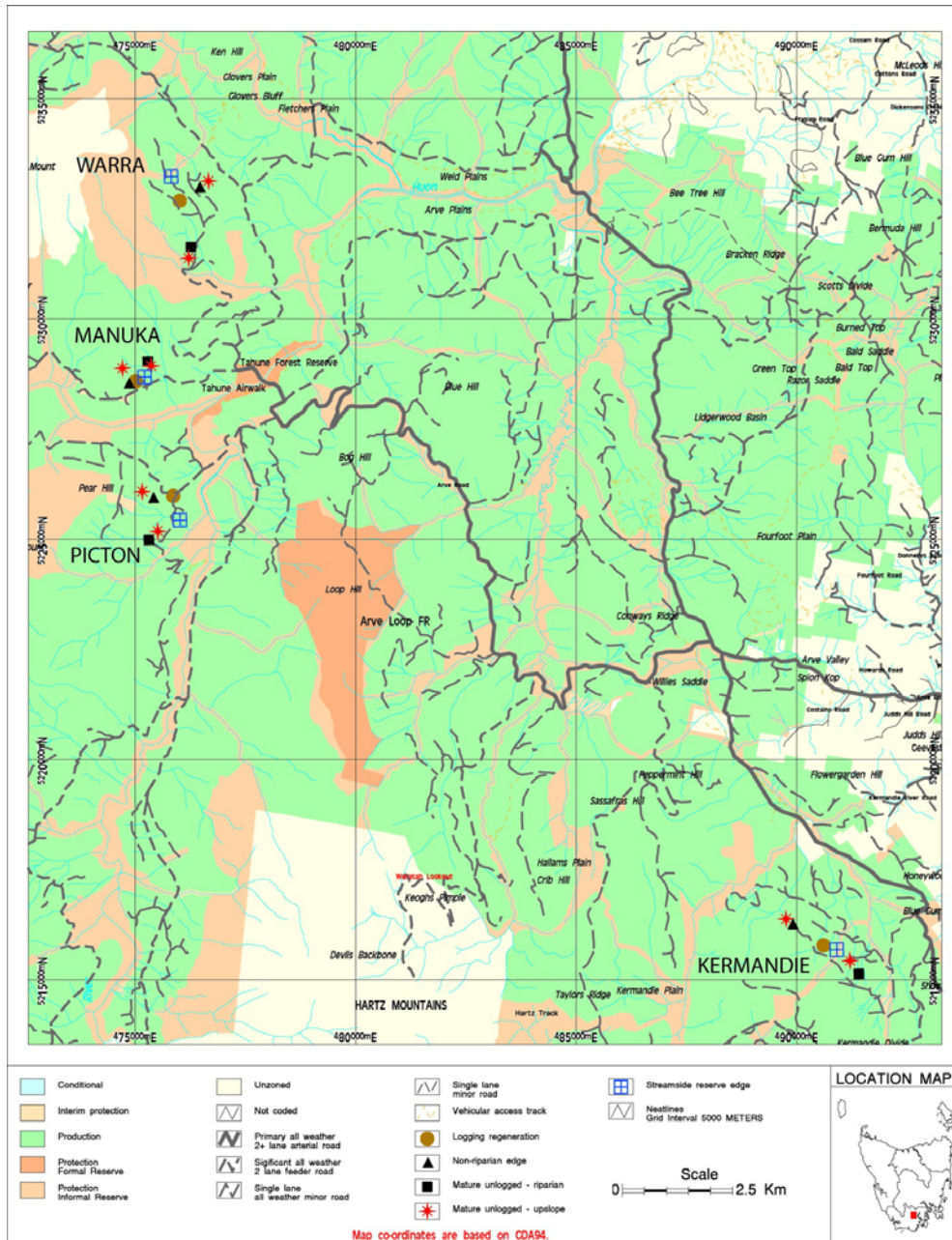


Figure 2. Schematic diagram of the site layout used in Trial 1. Three transects are randomly located in each of the five habitats. Data from mature forest interior (non-riparian) transects were used in Chapters 2, 4 and 5; mature forest interior riparian transects in Chapters 3, 4 and 7; coupe (regeneration) transects in Chapter 5; non-riparian coupe edges in Chapter 6; and streamside reserve coupe edges in Chapter 7.

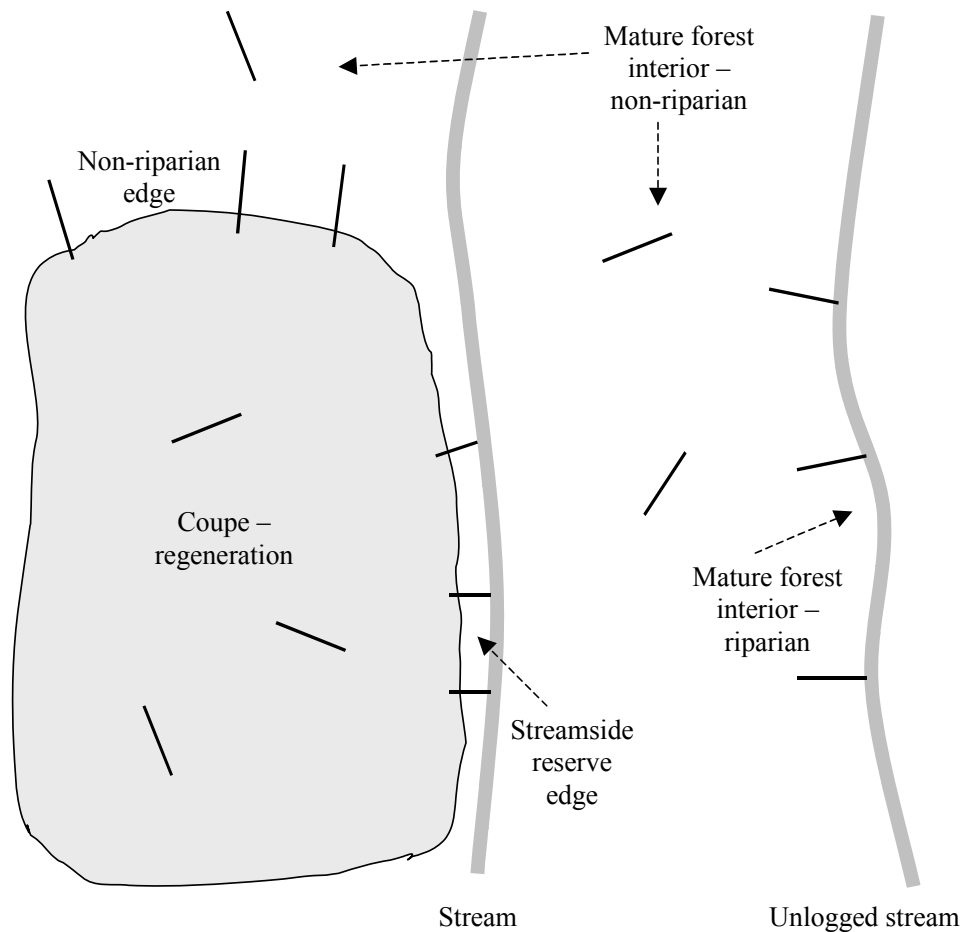
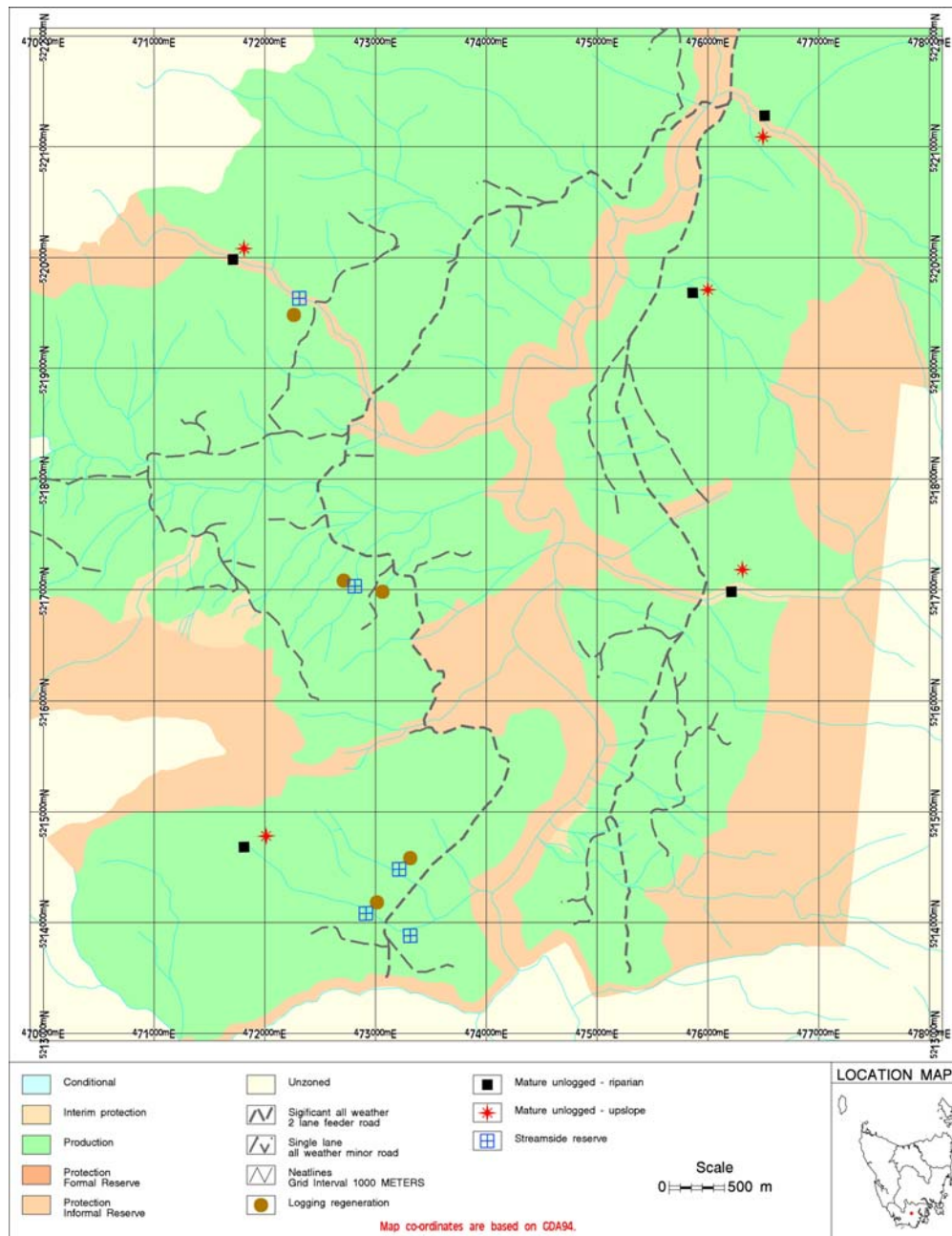


Figure 3. Location of the Trial 2 study area in southern Tasmania, showing the approximate locations of the five replicate stands representing the four habitat types: logging regeneration, mature unlogged – riparian, mature unlogged – upslope, and streamside reserves. Map prepared by Peter Ladaniwskyj from Forestry Tasmania.



Statement of co-authorship

I am the primary author on all manuscripts, having undertaken the data collection, data analysis, and chapter preparation. However, I have also acknowledged the contributions of others by recognising them as co-authors where applicable. The co-authors for each chapter are listed on the chapter title pages. Associate Professor Alastair Richardson and Dr Leon Barmuta (both School of Zoology, University of Tasmania) were my primary supervisors. They provided advice on survey design, statistical analysis of results, and commented on chapter drafts. Dr Leon Barmuta developed the statistical approach we used in Chapter 2. Dr Russell Thomson (Menzies Research Institute, University of Tasmania) is a biostatistician, and assisted with statistical analysis for Chapter 4. Dr Peter McQuillan (School of Geography and Environmental Studies, University of Tasmania) was a research supervisor for this Ph.D. program. He advised on survey methodology and beetle ecology, and edited drafts of Chapters 6 and 7. Dr Simon Grove (Forestry Tasmania) advised on the survey design for Chapter 8, and commented on drafts of several thesis chapters.

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Chapter 2

Evaluating spatial autocorrelation and depletion in pitfall-trap studies of environmental gradients

This chapter previously published as:

Baker, S.C. and Barmuta, L.A. (2006). Evaluating spatial autocorrelation and depletion in pitfall-trap studies of environmental gradients. *Journal of Insect Conservation* 10: 269-276.

Preface: This chapter tests whether the transect layout used in Trial 1, with unequal distances between pitfall traps in transects, is likely to produce patterns in beetles attributable to spatial autocorrelation or pitfall trap depletion.

Abstract

Studies of environmental gradients like edge effects commonly employ designs where samples are collected at unequal distances within transects. This approach risks confounding species patterns caused by the environmental gradient with patterns resulting from the spatial arrangement of the sampling scheme. Spatial autocorrelation and depletion (reduced catch) have the potential to influence pitfall trap collections of invertebrates. Readily available control data from a study of edge and riparian effects on forest litter beetles was used to assess autocorrelation and depletion effects. Data from control transects distant from the treatment transects located at habitat edges and streams were screened to determine whether the study design (pitfall traps at varying distances within transects) was imposing patterns on the data attributable to differential autocorrelation or depletion. Autocorrelation in species composition and assemblage structure was not detected within the 99 m transects. The abundance and species richness of beetles were not lower where traps were in closer proximity, indicating that the transect design was not causing measurable depletion or resulting in differential trap catch. These findings indicate that spatial autocorrelation and depletion are unlikely to impair further analyses of edge and riparian effects on litter beetles.

Key words: Coleoptera, Edge effects, Transects, Spatial structure, Species abundance pattern

Introduction

Sampling protocols with unequal distances between sampling points within transects are commonly employed in studies of environmental gradients, where sampling effort may be concentrated at one end of transects based on *a priori* assumptions of where impacts are most likely to occur. Examples include edge and ecotone effects studies (Bedford and Usher 1994, Didham et al. 1998, Kotze and Samways 2001, Dangerfield et al. 2003). Spatial effects are important to consider in any studies of community patterning, but are more likely to lead to erroneous trial conclusions when samples are taken at varying, rather than equal, distances. If not specifically accounted for, spatial effects can confuse patterns apparent from statistical analyses and lead to incorrect interpretation (Legendre 1993, Keitt et al. 2002).

Pitfall traps are the most widely used method of collecting ground-dwelling Coleoptera (e.g. Spence and Niemelä 1994, Rieske and Buss 2001, Ward et al. 2001, Perner and Schueler 2004). The advantages of using pitfall traps include their ease of construction and deployment and their capacity for lengthy trapping periods to obtain sufficient specimens for quantitative analyses. However the potential of trap proximity to result in either spatial autocorrelation of species assemblages (e.g. Sanderson et al. 1995, Niemelä et al. 1996), or depletion of the local invertebrate fauna (e.g. Luff 1975, Digweed et al. 1995, Ward, et al. 2001), tends to be ignored. These factors should be considered in the design and interpretation of pitfall trap studies along with other potential biases of this trapping method (Briggs 1961, Greenslade 1964, Luff 1968, Greenslade and Greenslade 1971, Greenslade 1973, Luff 1975, Spence and Niemelä 1994, Digweed et al. 1995, Melbourne 1999).

Spatial autocorrelation is an important factor which can affect invertebrate trap catches depending on the scale at which samples are taken (Sanderson, et al. 1995,

Leponce et al. 2004) and thus needs to be considered in relation to pitfall trap proximity within transects. Ecological distance (e.g. community dissimilarity) generally increases with geographical separation of samples (Sanderson, et al. 1995). Greater similarities in species composition with closer proximity may result from the local population dynamics and interspecific interactions of the insects themselves or from their response to external environmental processes (Legendre 1993, Wagner 2004). Spatial autocorrelation could arise from the relationship of the invertebrates with environmental factors (e.g. soil, vegetation) that are themselves spatially autocorrelated, or from other behaviours of the invertebrates such as their mobility, activity, or territoriality (Sanderson, et al. 1995, Wagner 2004).

Baker et al. (2004) found geographical separation of study sites to be a significant factor distinguishing litter beetle communities in Tasmania. Although the importance of distance to species turnover is implicit in calculation of β diversity (Magurran 2004), autocorrelation is rarely specifically tested at the spatial scale of sampling transects (Sanderson, et al. 1995). Niemelä et al. (1996) documented a slight (but non-significant) reduction in similarity of carabids, spiders and ants with increased sampling distance in mature forest, but did not detect distance effects in younger-successional forest. Sanderson et al. (1995) found spatial autocorrelation to be a factor in invertebrate community composition along transects. Leponce et al. (2004) documented reduced ant species richness from Winkler samples when the sampling interval was less than 10 m, a finding they attributed to spatial autocorrelation. Samples collected at varying distances within transects are therefore likely to exhibit varying degrees of spatial autocorrelation in the community patterning.

Depletion of the local invertebrate community is, to a certain extent, inevitable with destructive sampling methods such as pitfall trapping. Whether or not this

depletion significantly affects the interpretation of the data collected ought to be considered. The home range of invertebrates may overlap the location of more than one pitfall trap if these are placed in close proximity, resulting in reduced catch per trap (depletion) (Digweed, et al. 1995). Such depletion will almost certainly occur at different scales for different species (Digweed, et al. 1995, Ward, et al. 2001).

Depletion could also potentially result in fewer species per trap because of the relationship between abundance and species richness (Magurran 2004). Digweed (1995) trapped fewer individuals and species of carabids in poplar-spruce forest when pitfall trap clusters were more closely positioned. Ward et al. (2001) also recorded reduced species richness of beetles, especially of rarely trapped species, from closer inter-trap distances. In transects with unequal distances between traps, depletion effects could result in collection of fewer individuals or species where traps were in closer proximity.

The present study examines pitfall-trap proximity effects on Coleoptera from *Eucalyptus obliqua* forest in Tasmania, Australia, where pitfall trap placement along transects was unequal. The data are from control transects positioned away from known environmental gradients, but associated with studies of edge and riparian effects with equivalent transect layout. The aim of this study is to determine whether autocorrelation or depletion effects will confound analysis and interpretation of environmental gradients.

Methods

Study sites and sampling methodology

Four study sites were located in mature wet forest dominated by *Eucalyptus obliqua*, with mixed sclerophyllous and rainforest understorey. The study sites (Warra,

Manuka, Kermadie and Picton) were from 3 to 21 km distant from each other, and approximately 60 km south-west of Hobart in Tasmania, Australia (43°S 146°E).

The control sites were selected in forest away from known environmental gradients (riparian zones and edges of clearfelled logging areas). Three replicate transects of pitfall traps were randomly positioned within each of the four control sites. Each transect was 99 m long, with pitfall traps located at the following distances from starting points: 1 m, 5 m, 10 m, 25 m, 50 m and 100 m (72 traps in 12 transects). The treatment transects in the related edge and riparian effects studies had traps placed at these same distances from edges and streams.

Pitfall traps consisted of 7.5 cm diameter plastic drinking cups inserted in PVC downpipe sleeves dug into the soil. Ethylene glycol (antifreeze) was used as preservative. A plastic lid was held in place above each trap with three wooden sticks to protect traps from rainfall and disturbance by animals. Pitfall traps were closed for at least three weeks before trapping to avoid digging-in effects (Greenslade 1973). Traps were operated for three separate one-month periods: winter (June – July 2001), spring (October – November 2001) and summer/autumn (February – March 2002). All beetles were removed and identified to species or morphospecies.

Analyses

The dataset used in analyses consisted of 2,259 beetles from 194 morphospecies. Data from the three trapping periods were pooled for analysis. Statistical analyses were conducted in R Version 1.8.1 (R Development Core Team 2003).

Testing for spatial autocorrelation

The spatial autocorrelation analysis treated each sampling transect as a statistical replicate. To test for autocorrelation within transects, distance matrices were compared for a) Bray-Curtis dissimilarities of square-root transformed species abundance data for all 194 coleopteran species collected, and b) a matrix of the geographic distance (Euclidean, in metres) between pairs of pitfall traps. Square-root transformation was appropriate for the species-abundance data, which ranged between 0 and 10s of individuals collected per trap (Downes et al. 2002). Dissimilarity matrices were calculated with the 'vegdist' function from the Vegan library (Oksanen 2004). The dissimilarity matrices each were converted to a single vector with a third vector signifying the transect identity. The 'cor' function from the Base package of R was used to correlate vectors of the species and distance dissimilarity values. The 'boot' function from the Boot library was used to conduct a permutation test for whether the correlation coefficient is different than would be expected by chance with 499 different permutations of randomised reallocations of distances in the Euclidean distance vector (Davison and Hinkley 1997). The permutation test stratified the correlation by transect identity (12 replicate transects). The Spearman Rank Correlation coefficient provided an estimate of the degree of spatial autocorrelation. Unlike the Pearson coefficient, it does not assume a linear correlation structure, and should detect whether correlations were occurring among the closest traps even if there were no correlation between more distantly located traps. Visual interpretation of the standard normal quantile plot and a plot of the distribution of correlation coefficients assessed the assumption of normality of the permuted correlation distribution.

Testing for pitfall trap depletion

The data were compared between the six distances from the starting point using linear models with Gaussian (normal) errors. Consistently reduced abundance and/or species richness where traps were more closely located may imply a depletion effect caused by trap proximity. The model fitted abundance and species richness against linear and quadratic functions of distance (dist) and their interactions with sites:

$$Y = \log_e(\text{dist}) + \log_e(\text{dist})^2 + \text{site} + (\text{site} \times \log_e(\text{dist})) + (\text{site} \times \log_e(\text{dist})^2)$$

Y was either the \log_e transformed abundance, or the species richness of beetles.

Because site influences at the scale of several km are known to influence the beetle abundance, species richness and assemblage structure (Chapters 3 and 5; Baker, et al. 2004), we treated site as a blocking factor (fixed effect). Visual examination of plots of residuals versus fitted values, normal probability plots, and Cook's distance plots ensured the data met the assumptions of linear modelling.

Results and Discussion

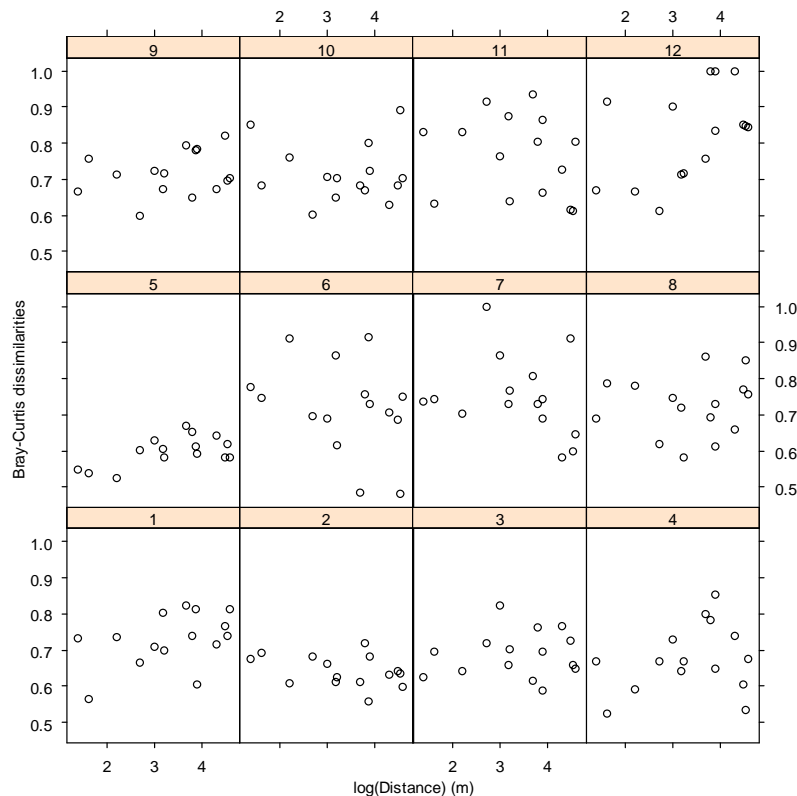
Autocorrelation test results

There is no evidence of spatial correlation within the 99 m transects (Bootstrapped correlation coefficient $r = 0.0101$; $P = 0.462$). This is illustrated in Figure 1, with no consistency among transects of patterns of Bray-Curtis community dissimilarities in relation to geographic distance between traps; i.e. beetle community dissimilarities were not consistently lower when traps were in closer proximity. Thus there is no evidence of more similar community composition when traps are in closer proximity. Analysis from control transects away from known environmental gradients indicated that spatial autocorrelation at the scale of our 99 m transects is unlikely to bias the interpretation of community gradients in the related edge and riparian effects studies.

Depletion test results

Site was the only significant term in the models of both the abundance and species richness of beetles collected in traps (Table 1). Figure 2 illustrates the variable nature of abundance and species richness recorded for each trap. While the site differences are evident (fewer beetles at Picton and greater numbers at Kermandie), there is no trend for lower numbers to the left of the distance axis where traps are located in closer proximity. These results confirm that there are site differences in beetle populations, but demonstrate that trap-catch is not affected by distance along transects. Since there were not fewer beetles or number of species of beetle when traps were in closer proximity, the sampling design appears not to result in detectable pitfall-trap depletion.

Figure 1. Community distance (Bray-Curtis) plotted against geographic distance between pairs of pitfall traps (\log_e transformed) for each of the twelve transects.

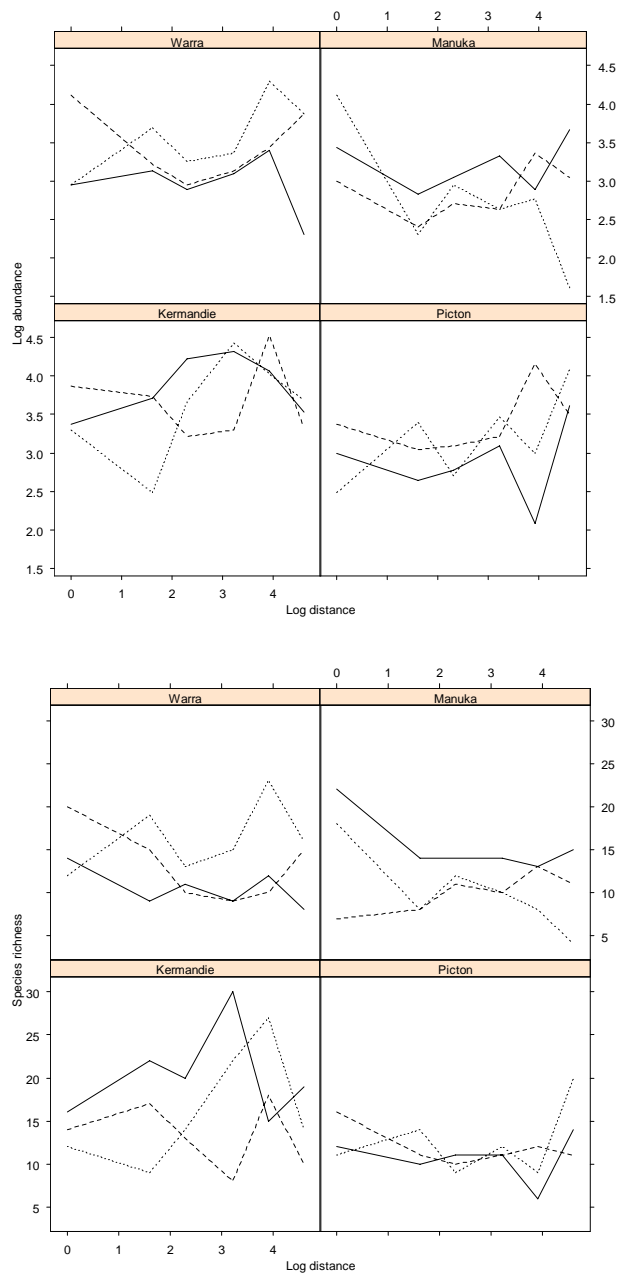


An additional complication is that different species will be influenced differentially, because of variation in mobility, habitat specificity, and within- and between-species interactions (e.g. Niemelä 1990, Davies et al. 2004). Thus, where sufficient single-species data are available to meet the distributional assumptions of analyses, testing species of differing size and mobility may be fruitful. In the present case, the high proportion of zero counts in pitfall catches (zero-inflation, Welsh et al. 1996) meant that single-species data did not meet the requirements for statistical analysis.

Table 1. The results of linear models on the abundance and species richness of beetles in relation to distance along transects and study sites.

Source of variation	\log_e (abundance)			Species richness		
	F	d.f.	P	F	d.f.	P
$\log_e(\text{dist})$	1.18	1	0.282	0.21	1	0.652
$\log_e(\text{dist})^2$	1.86	1	0.177	0.67	1	0.418
site	7.40	3	<0.001	4.83	3	0.004
$\log_e(\text{dist}) \times \text{site}$	1.62	3	0.195	0.96	3	0.417
$\log_e(\text{dist})^2 \times \text{site}$	0.70	3	0.559	1.09	3	0.359
error		60			60	

Figure 2. Abundance (\log_e transformed) and species richness of beetles from pitfall traps at six distances along transects at four study sites (site names in strips).



Practical application of findings

In this case, spatial autocorrelation and pitfall trap depletion were found not to be detectable at the scale of the transect layout. Thus our analyses of edge and riparian

effects on litter beetles are unlikely to be confounded by the transect design with unequal distances among pitfall traps. However, were spatial autocorrelation found to be a significant factor, then more similar community composition amongst traps placed closely together could lead to a false conclusion that the measured community change is a result of an underlying environmental gradient, when in fact it is simply a by-product of the sampling design. Likewise, pitfall depletion could erroneously lead one to conclude that fewer invertebrates occur near habitat edges or streams.

Since the control transects were randomly located in position and direction, and are located distant from streams and clearfelled forest edges which may create underlying environmental gradients, other extrinsic environmental influences which cause spatial organisation of the invertebrates (e.g. the presence of a canopy gap, a large rotting log, or a particular plant species) would be of variable influence among the different transects. It is possible that beetles may be more active near habitat edges, possibly leading to pitfall depletion or a spatial autocorrelation component to the 'edge effect'. Various statistical approaches may be adopted to either remove or explicitly model spatial autocorrelation in data analysis (Legendre 1993, Dalthorp 2004).

While we recognise that studies specifically intended to quantify the scale of spatial autocorrelation or pitfall trap depletion could be designed differently (e.g. Digweed, et al. 1995), this study illustrates how control data, already at hand in many designs of environmental gradient studies, can be used to either validate the project design or take remedial action if necessary. The potential for temporal depletion of invertebrates is another factor worthy of consideration, particularly in studies using continuous trapping over long periods. Pilot studies are obviously preferable since the main study design can be modified if depletion or strong spatial autocorrelation effects were detected; but when time and financial constraints preclude a pilot study,

testing control transect data from the main study is the next best option. This analysis approach is not only relevant to pitfall trap studies but would be relevant in any studies of environmental gradients.

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Chapter 3

Site effects outweigh riparian influences on ground-dwelling beetles adjacent to first order streams in wet eucalypt forest

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Preface: This chapter explores beetle assemblage patterns in mature forest interior riparian areas, and assesses the relative importance of riparian influences and site separation in structuring the beetle community.

Abstract

In wet eucalypt forest with a rainforest understorey the vegetation adjacent to first order streams does not form a distinct riparian strip. This study investigated the riparian response of terrestrial ground-dwelling beetles adjacent to four such streams in Tasmania, Australia. Beetle assemblages varied more between the four sites than they did with distance from stream within sites, where they exhibited a measurable but subtle riparian response. The extent of the riparian zone varied between the four study sites, with a 1-5 m riparian zone at three sites and a gradually changing community up to 50-100 m upslope at one site. There was a trend for greater between plot variability immediately adjacent to the streams, possibly because this is a more highly disturbed environment. None of the habitat variables measured were consistently associated with riparian or upslope assemblages of beetles, probably explaining the subtlety of the beetles' riparian response. Forest conservation efforts for terrestrial species should not necessarily be focused on the riparian zone in preference to upslope areas.

Key words: riparian zone width, site effects, upslope habitat, headwater streams, terrestrial beetles, pitfall trapping

Introduction

The riparian zone is an interface between the aquatic and terrestrial environments, and forms an ecotone in which elevated water tables, buffered microclimatic conditions and distinct vegetation communities (Naiman et al. 1993) often provide favourable habitat for animals (e.g. Bentley and Catterall 1997; Brenner 2000; Catterall 1993; Catterall et al. 2001; Woinarski and Ash 2002). Put simply, ‘riparian’ can be defined as “affected by the river” (Malanson 1993); the riparian zone may be very noticeable, defined by an obvious band of vegetation, or alternatively the vegetation may be the same as that of upslope areas (Malanson 1993). Plant species distribution is generally used to define the boundaries of the riparian zone (Brinson and Verhoeven 1999; Naiman et al. 1998), with the result that an a priori judgment of riparian zone width based on vegetation has been implicit in some studies comparing riparian to upslope conditions (e.g. Brenner 2000; Everett et al. 2003). This approach may be valid in some systems where the change in vegetation is abrupt, however different ecological processes and biotic communities may behave differently (Gregory et al. 1991), and perhaps a better approach is to define the riparian zone specific to the study group of interest by sampling at various distances from the stream. Miller (2000) notes that while vegetation may be the most obvious physical representation of an ecosystem, suitable habitat is a species-specific concept concerning the particular resources and environmental conditions that allow a species to survive and reproduce.

The present study of ground-dwelling Coleoptera attempts to determine the extent of the riparian zone adjacent to first order streams in wet forest dominated by *Eucalyptus obliqua* in Tasmania, Australia. For these streams, the riparian zone cannot be defined in terms of vegetation, which tends not to vary obviously with

distance from stream. Indeed, vegetation is not always a good surrogate for the habitat of other components of the biota, such as invertebrate groups (Mac Nally et al. 2002; Oliver et al. 1998; Taylor et al. 1994), which have the potential to form distinct riparian and upslope species assemblages in response to subtle changes in habitat conditions, such as transitions in soil moisture and humidity (Brinson and Verhoeven 1999; Hutchens and Wallace 2002; Levings and Windsor 1984; Lynch et al. 2002; Marra and Edmonds 1998; Niemelä et al. 1992; Richardson and Devitt 1984; Wang et al. 2001). For example, Kremen (1992) found distinct butterfly, but not plant, communities at streamsides and ridges in Madagascar.

Ground-dwelling beetles are exceptionally diverse, and vary greatly in their size, food requirements and trophic stages, dispersal abilities, habitat requirements and specificity (Didham et al. 1998; Lawrence and Britton 1994; Niemelä et al. 1993). This makes these beetles useful to study, because at least some species are likely to be sensitive to riparian conditions. Some beetles, for example many Scirtidae, have an aquatic larval and terrestrial adult stage and are therefore likely to inhabit the riparian zone (Erman 1984; Lawrence 1992).

In subtropical eucalypt forest in Queensland, Australia, Catterall et al. (2001) showed communities of litter invertebrates (including beetles) in riparian and upslope plots to be biotically more distinct than different sites of matched landscape position, suggesting that riparian influences were of greater significance than geographical separation. Disturbance by periodic flooding can lead to high diversity of habitat conditions along the length of a watercourse that may result in greater species diversity than in the more uniform upslope habitat (Brinson and Verhoeven 1999; Gregory et al. 1991; Naiman and Décamps 1997). We proposed the following hypotheses about the way in which the ground-dwelling beetle community responds to riparian attributes adjacent to small streams in cool-temperate wet eucalypt forest:

1. The gradient from the riparian zone to upslope will be more important than site differences in structuring the beetle community.
2. There will be greater community diversity between different positions located along the streambanks, where disturbance by flooding is likely to cause greater diversity in habitat conditions, than in undisturbed forest away from the streams.

Methods

Study sites

We examined riparian zones for terrestrial ground-dwelling beetle communities adjacent to four streams in southern Tasmania, Australia. The streams flow through unlogged forest at four sites in the Huon (Leas Creek and King Creek), Picton (Isabel Creek), and Kermadie (Crittter Creek) River valleys, approximately 60 km WSW of Hobart, Tasmania (Table 1). Leas Creek and King Creek were located within the Warra long term ecological research site (Brown et al. 2001). We chose small-sized perennial first order streams representative of the ranges of size, channel morphology, and bank slopes of streams which would be reserved under the Forest Practices Code (Forest Practices Board 2000). The streams varied in size, channel morphology, and slope of the stream-banks (Table 1).

This “wet” forest-type consists of a *Eucalyptus obliqua* overstorey with a mixed understorey of thamnic rainforest and sclerophyllous species (Neyland 2001). Unlike drier forest communities, there was no obvious delineation between the vegetation in the riparian zone and upslope forest. Nor was there evidence of different fire histories in the riparian and upslope forest based on the sizes of dominant trees or mapped boundaries of forest structure based on aerial photo interpretation (Forestry Tasmania GIS maps, Stone 1998).

A pilot study (unpublished data) compared ground-dwelling beetle assemblages between single transects within three streamside-buffers, one on sedimentary and two on dolerite-derived soils. Ordination indicated that the sedimentary site had quite similar beetle assemblages to one of the dolerite sites while the other dolerite site was more distinct. Based on this pilot study both sedimentary (Isabel Creek) and dolerite (King, Leas and Critter Creeks) derived soil types were included in the current survey. Both the sedimentary and dolerite soils supporting this forest composition are generally well-drained (Laffan 2001).

Isabel Creek was significantly larger than the other three streams and had an approximately 10 m high waterfall 35 m upstream of the closest study transect. Isabel and King Creeks were wider, had greater water flow, and much steeper stream banks than Leas or Critter Creeks (Table 1). Leas Creek and Critter Creek flowed underground for part of their courses, particularly the multi-channelled Leas Creek, which was occasionally visible where a sedimentary outcrop forced water to the surface. Sub-surface flow is common in Tasmanian soils formed in dolerite. In dolerite terrain some stream channels are inferred to follow pathways that existed before Holocene soil formation (McIntosh 2001).

Part of the King Creek catchment upstream of the study site had been logged in 1997 and part of the Critter Creek catchment had been logged in 1991. No recent logging had occurred in the Isabel or Leas Creek catchments, although some selective logging of the best trees might have occurred in all study areas prior to 1960 (Hickey et al. 2001).

A weather station near the Leas Creek site recorded approximately 1300 mm of rainfall, and average monthly temperatures ranging from -0.5 to 4.8°C (minimum) and 11.8 to 31.3°C (maximum) over the period June 2001 – May 2002 (Forestry

Tasmania; unpublished data). Rainfall varied seasonally, with much drier conditions during summer-autumn. A hydrological study of streams in the Warra LTER, including King Creek, found rapid increases in stream flows following storm events, although lags in discharge were greater in summer and autumn when soils were drier (Ringrose et al. 2001).

Sampling methods

At each site, three replicate transects of pitfall traps were established at right angles to the stream channel. Transects were randomly positioned at least 100 m from roads or logging coupes to avoid confounding with edge effects, and with at least 25 m separating adjacent transects. Transects were located at positions where streams had clearly identifiable surface water. Beetles were collected using pitfall traps; a single pitfall trap was located at 1 m, 5 m, 10 m, 25 m, 50 m and 100 m from the stream (72 traps). Traps were operated continuously during three separate one-month periods: winter (June – July 2001), spring (October – November 2001) and summer-autumn (February – March 2002). These periods were spaced four months apart over a twelve-month period in order to account for seasonality in beetle activity. The pitfall traps consisted of 225 mL plastic cups suspended in PVC downpipe sleeves (7.5 cm external diameter, 10 cm deep). The cups were filled to 4 cm depth with ethylene glycol (antifreeze) as a preservative. A 12 cm diameter plastic lid was held approximately 3 cm above each trap with three wooden sticks to protect the traps from rainfall and disturbance. Pitfall trap depletion and spatial autocorrelation effects from the transect design were tested, and were not found to influence the beetles collected (Chapter 2).

Beetles were sorted to family and morphospecies based on external morphology, using keys to family in Lawrence and Britton (1994) and Lawrence et al. (1999). Taxonomic knowledge of many beetle families is scarce, and identification to taxonomic species was not possible for all morphospecies. Species identifications were made by reference to the Forestry Tasmania TFIC Insect Collection, where the reference collection will be deposited.

Habitat variables considered potentially important in influencing beetle distributions (Baker 2000) were recorded at each pitfall trap location. Variables included the geographical factors aspect, slope (%) and distance from stream (m); the soil factors % moisture content, bulk density, loss on ignition (LOI); and from 1 x 1 m square quadrats, the vegetation factors % tree roots, % bryophytes, % fungi, % dead fern fronds, % tree stem, % understorey plant, % *Dicksonia* stem; and the litter layer factors % mineral soil, % rock, % coarse woody debris, % fine woody debris, % O2 litter, and % O1 litter. Litter depth was calculated as the average of 4 measurements from the quarters of the quadrat square. Percentage canopy cover was estimated from digital hemispherical photographs taken at ground level adjacent to each pitfall trap (Frazer et al. 1999). Percentage coarse woody debris was estimated from larger (4 m x 4 m) plots. Soil samples were collected with a 5 cm depth bulk density corer from the location where the pitfall trap was subsequently placed. Not all soil moisture measurements were comparable, because of potential confounding with rainfall events between collection dates. All soil samples at Isabel Creek were collected on 8 May 2000, and at King Creek on 29 May 2000. Soils were collected from two transects at Leas Creek on 24 April 2000 and from one transect on 22 May 2000; and from two transects at Critter Creek on 27 April 2000 and one transect on 4 May 2000.

Statistical analyses*Seasonality of riparian response*

Seasonal sub-sampling aimed to trap a reasonable representation of those species present during an annual cycle rather than assessing seasonal or inter-annual patterns in abundance for individual species. It was intended that data from the three pitfall trapping rounds be lumped for each trap to reduce the proportion of zeros and improve the dataset for community analyses. However, the seasonal data were initially tested to check whether riparian zone assemblages shifted seasonally, since Brenner (2000) found that riparian and upslope beetle communities were more distinct in spring and early summer when moisture gradients were likely to have been greater. Non-parametric multivariate analysis of variance (NPMANOVA, Anderson 2001; Anderson 2003c) was used to test beetle assemblages for a multivariate interaction between “season” and “distance from stream” at each site, using a two-way crossed model. “Season” (winter, spring, summer-autumn samples) and “Distance” (1 m, 5 m, 10 m, 25 m, 50 m and 100 m from stream) were fixed factors (Downes et al. 2002). This and subsequent analyses were conducted on square-root transformed data using Bray-Curtis dissimilarities and 9999 unrestricted random permutations of the raw data, where the three transects at each site were considered replicates. Rare species (defined for this and subsequent analyses as those recorded only from single samples or of abundance less than 0.5% of the total abundance) were omitted. For analysis of seasonality there were 34 species at Isabel Creek, 32 for King Creek, 34 for Leas Creek and 37 for Critter Creek sites after omission of rare species. Subsequent analyses were based on pooled data from the three seasons.

Analyses of site and distance effects on ground-dwelling beetle assemblages

NPMANOVA and NPDISP (a test for multivariate dispersion, (Anderson 2003b)) were then used to test the response of beetle assemblages to distance from stream and study sites. NPDISP analysis tests for differences in dispersion (different degrees of scatter) of treatment groups (Anderson 2003b). For these analyses, omission of rare species reduced the dataset from 2,021 beetles and 173 morphospecies to 1,679 beetles from 37 morphospecies.

NMS (non-metric multidimensional scaling) ordination was used to investigate whether site or distance from stream were more important in structuring the beetle species assemblages. This was conducted in PC-ORD Version 4.10 (McCune and Mefford 1999) in “Slow and Thorough” autopilot mode on pooled data from the three replicate traps at each distance from stream within sites. Data were square root transformed and the Bray-Curtis (Sørensen) distance measure was used.

Site-specific analyses

Both CAP (canonical analysis of principal coordinates) and NMS ordinations were conducted separately on beetle assemblages from the four study sites, in addition to one-way NPMANOVA and NPDISP analyses to test distance effects. The average dissimilarities within distance from stream groupings were calculated by NPMANOVA. CAP is a constrained ordination approach that displays multivariate data by reference to specific *a priori* hypotheses (Anderson 2003a; Anderson and Willis 2003). This approach can reveal patterns that may be masked in unconstrained NMS ordination (Anderson and Willis 2003; Økland 1996). P-values from permutation tests for two test statistics, δ^2 (first squared canonical correlation) and a Trace Statistic, test for group differences in CAP analysis (Anderson and Robinson 2003; Anderson and Willis 2003). In addition, correlation of species with canonical

axes in CAP analysis can be used to identify species responsible for multivariate patterns. The strength of treatment patterns can be assessed by classification success of *a priori* treatments with the “leave-one-out” allocation success procedure (Anderson and Willis 2003). The number of principal coordinate axes (m) to be used in the CAP analysis was calculated by the computer program, and 9999 random permutations were used for the permutation test. NMS ordinations were also conducted for site-specific datasets. Joint plots for NMS ordinations were overlaid for correlated environmental variables with $r^2 > 0.2$ within the ordination space. Omission of rare species from these datasets left 35 morphospecies for Isabel Creek, 31 for King Creek, 32 for Leas and 36 morphospecies for Critter Creek.

Results

A total of 2,021 beetles were trapped, representing 173 morphospecies (ms) from 26 families. The Staphylinidae were the most abundant family trapped: 797 beetles (55 ms) of which 610 (26 ms) were from the sub-family Aleocharinae. The Leiodidae (399 beetles, 21 ms), Curculionidae (366 beetles, 28 ms) and the Carabidae (258 beetles, 11 ms) were the next most numerous families. Aquatic species, in particular, may be more common in riparian areas. Beetles from two families that usually have aquatic larvae were collected; a single Elmidae (*Notriolus* sp.) was collected in a trap 1 m from Critter Creek, while 8 specimens from 4 morphospecies of Scirtidae were collected from traps 1-10 m from King, Isabel and Leas Creeks. In related edge effects trials (unpublished data), the same scirtid morphospecies were also trapped distant from streams, usually at poorly drained firebreaks at the edges of logged areas, and may also use wet rotting logs as larval habitat (Yee 2005) indicating that they are not riparian specialists. The only other elmid trapped (*Simsonia* sp.) was

collected 1 m from a stream in a streamside reserve, in correspondence with the more specialist aquatic existence of Elmidae (J. Gooderham, pers. comm.).

Seasonality of riparian response

Beetle assemblages differed significantly between trapping seasons at all study sites (Table 2). Although there were changes in the composition of beetle assemblages between sample dates, there was no significant interaction between trapping season and distance from stream at any of the four study sites (Table 2). This indicates that beetle assemblages did not shift seasonally with respect to distance from stream, and justifies pooling samples from the three seasons for subsequent analyses.

Site and distance effects

Multispecies assemblages of beetles varied with distance from stream differently at the different sites. The Site x Distance interaction was significant in NPMANOVA ($F_{15, 48} = 1.300$, $P = 0.009$) and NPDISP ($F_{15, 48} = 2.731$, $P = 0.004$) analyses. An ordination based on pooled data from each distance from stream within sites (Figure 1) shows that beetles respond far more strongly to site differences than they do to distance from stream. Because of clear overall site differences in beetle assemblages, and the differing response of beetles to distance from stream at different sites, subsequent analyses are presented on a site-by-site basis.

Table 1. Characteristics of the sites and the streams (mean \pm SD).

Site	Location	Elevation	Landform	Stream type	Floodplain width	Combined channel width	Slope of bank	Slope of stream	Aspect
Isabel Creek	43°7'42''S 146°41'44''E	150 m	Permian sedimentary	aboveground, braided	7.0 \pm 2.5 m	4.9 \pm 1.1 m	39 \pm 21%	12%	S
King Creek	43°4'13''S 146°42'31''E	400 m	Jurassic dolerite	aboveground	3.7 \pm 1.7 m	2.3 \pm 1.2 m	28 \pm 9 %	13%	E-ESE
Leas Creek	43°5'35''S 146°41'50''E	200 m	Jurassic dolerite	largely underground, braided	8.7 \pm 4.3 m	undetermined as underground	50 \pm 13% (tending downslope beyond 10 m)	43%	S
Critter Creek	43°13'3''S 146°53'44''E	300 m	Jurassic dolerite	partly underground	2.0 \pm 0.6 m	1.1 \pm 0.4 m	12 \pm 5%	9%	NNW-NE

Table 2. NPMANOVA for litter beetle assemblages at the four study sites over three seasons and six distances from streams.

Source	Study Site							
	Isabel Creek		King Creek		Leas Creek		Crittter Creek	
	MS	F	MS	F	MS	F	MS	F
Season	18078.6	5.7994***	15658.4	4.8255***	10383.64	2.4641***	15533.23	5.1339***
Distance	4481.472	1.4376*	6258.844	1.9288***	4444.807	1.0548 [#]	5745.271	1.8989 [#]
Season x Distance	3190.443	1.0235 [#]	3909.43	1.2048 [^]	3299.903	0.7831 [#]	3038.998	1.0044 [#]
Residual	3117.323		3244.958		4213.898		3025.603	

Significance levels [#]p ≥0.1; [^]p <0.1; *p <0.05; **p <0.01; ***p <0.001.

d.f.: Season = 2, Distance = 5, Season x Distance = 10, Residual = 53

Site based analysis

Distance from stream was found to be a significant factor influencing beetle assemblage compositions at Isabel Creek ($p = 0.003$) and King Creek ($p = 0.008$), but not Leas Creek ($p = 0.534$) or Critter Creek ($p = 0.115$) sites in NPMANOVA analyses (Table 3). The non-significance of NPDISP analyses at Isabel and King Creeks (Table 3) indicates that group differences result from differences in location of treatment groups in multidimensional space rather than differences in dispersion. Community dispersion was found to differ significantly in relation to distance from stream only at Critter Creek (NPDISP $p = 0.016$; Table 3). There was insufficient power in NPMANOVA and NPDISP analyses to identify where along the riparian transects community differences arose with pair-wise comparisons. However, high within group dissimilarities for plots 1 m from Critter Creek (84% compared to 48 - 67% for distances further upslope; Table 4) probably caused the significant treatment difference in NPDISP. Variability in beetle assemblages was also highest immediately adjacent to Isabel and King Creeks, but not at Leas Creek (Table 4).

Table 3. Non-parametric multivariate analysis of variance (NPMANOVA) and analysis of dispersion (NPDISP) of distance effects on litter beetle assemblages at four study sites.

Site	NPMANOVA			NPDISP		
	MS	MS	F	MS	MS	F
	Distance	Residual		Distance	Residual	
Isabel Creek	3468.313	1728.821	2.0062**	69.7592	36.7616	1.8976 [#]
King Creek	3660.965	2293.943	1.5959**	90.5661	47.3532	1.9126 [#]
Leas Creek	3230.126	3316.265	0.974 [#]	94.0052	43.7199	2.1502 [#]
Critter Creek	2598.222	2104.24	1.2348 [#]	143.1425	32.5312	4.4002*

Significance levels [#] $P \geq 0.1$; [^] $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

d.f.: Distance = 5, Residual = 12.

Figure 1. NMS ordination of sites and distances from streams. Stress = 12.5% and Instability = 0.05105 for 3-d solution after 400 iterations. Site codes are followed by distance from stream in meters. Squares are Isabel Creek; triangles are King Creek; crosses are Leas Creek; diamonds are Critter Creek.

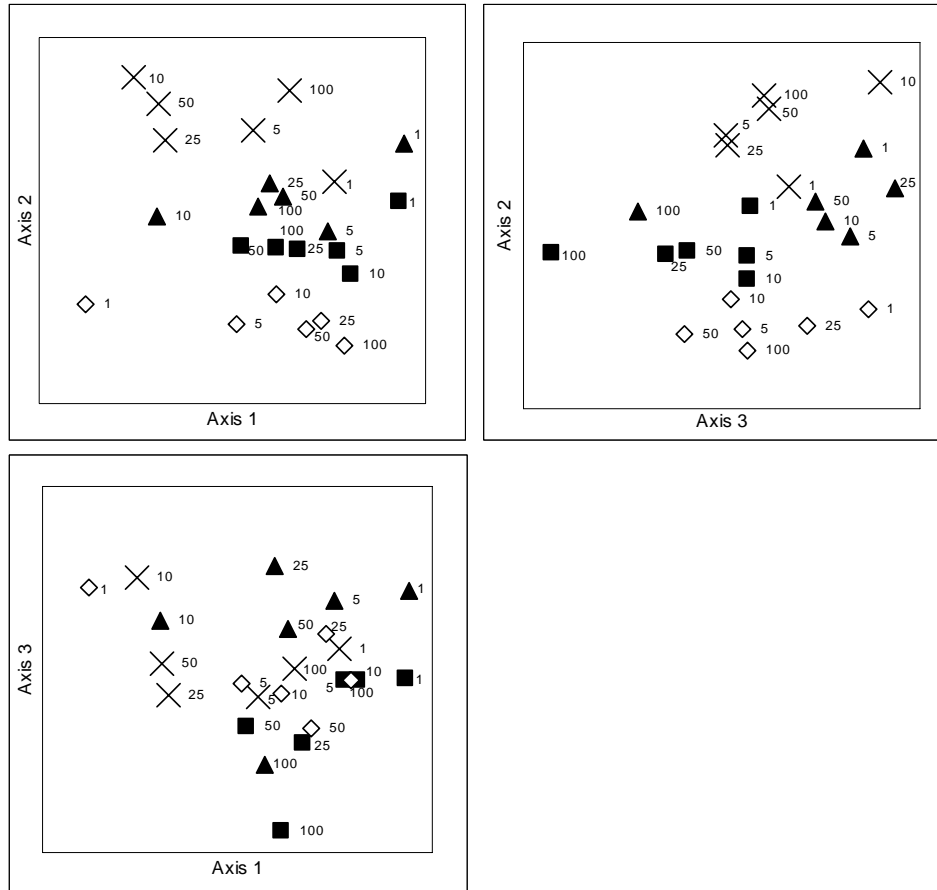


Table 4. Average dissimilarities (%) in litter beetle assemblages within groups of plots at different distances from streams at each study site.

Site	Distance					
	1 m	5 m	10 m	25 m	50 m	100 m
Isabel Creek	69.0	52.1	67.1	53.9	51.6	51.5
King Creek	80.7	72.7	62.5	66.9	53.0	64.0
Leas Creek	74.9	66.8	90.6	77.1	92.3	80.6
Critter Creek	83.8	62.3	63.7	48.3	55.8	67.1

CAP test results (Table 5) corroborate those of the NPMANOVA analysis for Isabel, Critter and Leas Creek sites but not for King Creek, for which distance from stream categories were non-significant with CAP. The percentage of pitfall traps re-allocated correctly into distance from stream groupings in the leave-one-out allocations was generally low (Table 5). At Isabel Creek (69%) and Leas Creek (60%), a large proportion of the mis-classifications were into adjacent distance categories, suggesting that while the characteristics of beetle assemblages are not distinct for the discrete distances from stream indicated by the treatment groups, assemblages show a transitional change with distance from stream. However, mis-classifications into adjacent distance categories were infrequent at King Creek (29%) and Critter Creek (33%) indicating weaker relationships with distance from stream.

CAP constrained ordination plots (Figure 2) were useful in illustrating the response of beetle assemblages to the riparian–upslope transition at each study site. These ordination plots were indicative of at least some response to riparian factors at each of the four study sites, although, as suggested by the poor leave-one-out allocation success rates, beetle community response appeared not to be consistent across the three transects for particular distances from streams. The strongest riparian

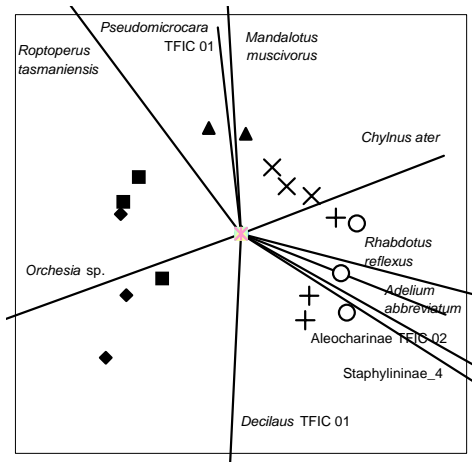
response was at Isabel Creek where the CAP plot indicates a transition in beetle assemblages corresponding with an increase in distance from the stream to 50-100 m upslope. At the other three sites, the CAP plots illustrate different beetle assemblage composition for 1 m plots together with some, but not all, 5 m plots, with no patterning further upslope. Vectors for species highly correlated with plot positions in the ordination space illustrate which species correlate with riparian or upslope plots. These patterns are site-specific rather than being consistent across sites, suggesting that commonly trapped species were neither riparian nor upslope specialists. Overall, riparian plots are more characterized by the lack of certain species rather than by preference by many species. Other than the carabid *Pogonoschema robustum* (Sloane, 1920), for which there is little distributional data, the species correlated with riparian plots (Figure 2) were commonly trapped away from streams and are unlikely to be riparian specialists (SC Baker, unpublished data; TFIC database records, unpublished data).

Table 5. CAP results testing for differences in beetle assemblages between distance from stream categories at each study site.

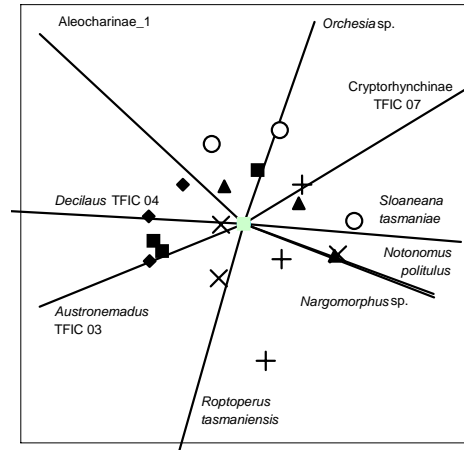
Site	Test statistics				m	Leave-one-out success (%)
	Trace	P-value	δ^2	P-value		
Isabel Creek	1.830	0.1125	0.9761	0.0003	5	27.8
King Creek	1.558	0.0752	0.6873	0.2950	4	22.2
Leas Creek	1.095	0.6091	0.5662	0.6395	4	16.7
Critter Creek	1.542	0.0826	0.7689	0.1161	4	16.7

Figure 2. Constrained CAP ordinations of litter beetle assemblages from 6 distances from the stream at each study site. Correlation vectors are overlaid for morphospecies with $|r| > 0.5$ with either of the canonical axes. Diamonds are 1 m plots, squares 5 m, triangles 10 m, crosses 25 m, pluses 50 m and circles 100 m plots.

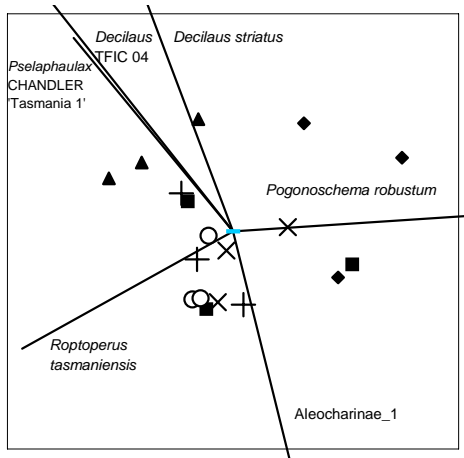
Isabel Creek



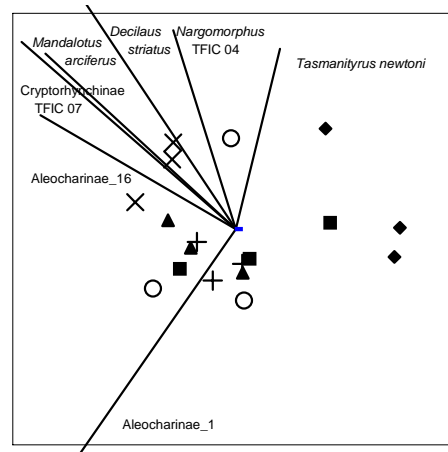
Leas Creek



King Creek



Crittter Creek



NMS ordinations (not presented) were not as useful as the CAP constrained ordinations in illustrating the riparian response of beetles, although the response of beetles to distance from stream was still apparent. The correlations of habitat variables with the beetles' assemblage structure were rather weak and inconsistent between sites. The most strongly correlated factor was distance from stream at Isabel Creek ($r^2 > 0.7$). Distance was also correlated with Critter Creek and King Creek ordinations, but not for Leas Creek. Certain other habitat variables appeared correlated with riparian communities on site-specific bases; litter depth at Critter Creek, soil organic matter (LOI) and moisture at Leas Creek, tree stem and bryophyte cover at Isabel Creek. Other habitat factors appeared to correlate with certain assemblages of beetles without appearing to relate to the distance from stream. Soil moisture content (Appendix 3) was highly variable and did not appear to be related to distance upslope from the streams within sites, with the possible exception of Leas Creek, although the correlation was probably caused by unusually high moisture content at a single plot 1m from the stream.

Discussion

The results indicate a subtle response of ground-dwelling beetles to riparian zones adjacent to first order streams in wet eucalypt forest. Beetle assemblages, and the magnitude of their riparian response varied between the four study sites, with an approximately 1-5 m riparian zone at three sites and a gradually changing community up to 50-100 m upslope at one site. Abundance and diversity of beetles in the riparian-upslope transition are explored elsewhere (Chapter 4). Closer positioning of pitfall traps near to streams in future studies could better define the scale of the riparian response. Since pitfall trappability is affected by species' activity levels and

behaviour (Greenslade 1964; Melbourne 1999), some ground-dwelling beetle species may not have been effectively sampled, and combined use of pitfall traps with litter extraction may potentially have sampled additional sensitive species (Fisher 1999; Rieske and Buss 2001).

Site effects were much more important than riparian effects in structuring the beetle communities, with significant variation in the species assemblages between sites. This result contrasts with Catterall *et al.*'s (2001) findings that various flora and fauna assemblages including litter invertebrates were more similar across riparian sites than between paired riparian and upslope areas. Different riparian and upslope vegetation in their subtropical environment probably points to greater disparity in environmental conditions than in our study, and may explain the contrasting results. The greater geographical separation of sites in the present study (up to approximately 13 km compared to only 1.5 km with Catterall *et al.* (2001)) is probably also a factor in the greater community turnover between sites. Site differences possibly relate to factors including the intrinsic patchiness of beetle occurrence (Niemelä *et al.* 1986; Niemelä *et al.* 1992), the geographical separation of sites and species turnover (Gering *et al.* 2003; Summerville *et al.* 2003), possible differences in fire history (frequency, intensity) and stand characteristics, a different soil type and a microclimate influenced by a waterfall in the case of the Isabel Creek site, and a 250 m elevation range. However, the beetle assemblage at the sedimentary Isabel Creek site fell within the range of assemblages at the three dolerite-derived sites (Fig. 1) suggesting that ground-dwelling beetles were not differentiating sites according to soil parent material. Geographical separation of sites was identified as an important factor patterning litter beetle assemblages in another study at a similar spatial scale in the same region (Baker *et al.* 2004).

The riparian response of ground-dwelling beetles was found to be site specific, even within a relatively uniform vegetation type and amongst first order streams. The largest stream, Isabel Creek, had the greatest riparian response, with a community gradient extending 50-100 m from the stream. This most likely relates to the influence of a waterfall at this site, creating a stronger environmental gradient, with moister conditions lower in the profile, which is also indicated by a lower proportion of *E. obliqua* nearer the stream. In contrast, the King Creek site exhibited a much more subtle community riparian response of only 1-5 m in spite of an aboveground stream and steep stream-banks. Beetle assemblages also had a 1-5 m riparian response to the two smallest streams that flowed partially underground at Critter and Leas Creeks. The much greater riparian response at Isabel Creek warns that beetles will not show a uniform response to all first order streams. Some streams will have stronger riparian characteristics as a result of topography, microclimate or geomorphology; influences worthy of further research. The finding that riparian response varied between sites should be considered in the design and analysis of similar studies. The spatial scale at which replicates are taken could influence conclusions (Knopf and Samson 1994), with variation in riparian response between sites potentially confounding results in studies which use sites as replicates without testing for site x distance interaction (e.g. Lynch et al. 2002).

Field Code Changed

Between plot variability in beetle assemblages was greatest 1 m from streams at King, Isabel and Critter Creeks, although this pattern did not hold true at Leas Creek, and the statistical test for differences in dispersion was only significant at Critter Creek. In peak flow conditions, areas 1 m from the stream banks were occasionally flooded, but it is unlikely that flood-waters would have reached as far as 5 m upslope. Greater variability could arise from greater diversity in habitat conditions as a result of periodic flooding disturbance (Gregory et al. 1991; Pollock

1998), or as a symptom of a stressed environment (Warwick and Clarke 1993). Soil and litter conditions were correlated with positioning of riparian plots in ordinations, but varied between sites. The factor 'distance from stream' was also correlated in the direction of upslope plots at Isabel, King and Critter Creeks, providing additional evidence for riparian effects at these sites. We found that the extent of the riparian zone did not shift seasonally, in contrast to litter beetles in Oregon (Brenner 2000) which possibly shifted in response to changing moisture gradients. Elevated soil moisture is usually considered important in distinguishing riparian and upslope communities; yet at these sites it was higher than average at only one plot 1 m from the stream at Leas Creek. Soil was collected only once during a wet period, and rainfall patterns were very different between the three trapping seasons, suggesting that seasonal changes in moisture gradients are a possibility (see Ringrose et al. 2001), even if not to such an extent that beetle shift in response.

Further research into other plant and animal groups in mixed wet forest is required to determine whether other taxa respond more strongly to riparian characteristics. For example, bird assemblages had greater abundance and species richness in riparian than slope sites elsewhere in Tasmania (MacDonald et al. 2002). Likewise, future studies of riparian zones adjacent to higher order streams and rivers would be valuable since response of beetles may well be greater than for the first order streams investigated here. Nevertheless, understanding the dynamics of low order streams is important to our understanding of forest function, since low order streams are dominant in terms of the land area influenced. This topic is important since these forests are clearfell harvested for timber with only narrow streamside reserves (depending on catchment area) to protect riparian values (Forest Practices Board 2000). That site effects were greater than riparian effects suggests that

conservation efforts for terrestrial beetles need to be spread throughout the forest landscape, as community changes were apparent within only a few kilometers.

Conclusions

Site differences rather than riparian zone differences were more important in structuring the beetle communities in this study, in contrast to our hypothesis based on the findings of Catterall *et al.* (2001). This study indicated that ground-dwelling beetle assemblages adjacent to first order streams in wet forest showed subtle community transition in response to the stream. A 1-5 m riparian zone affected beetles at three of four sites. One site had a wider riparian zone, with a transition in the beetle community to 50-100 m upslope, probably as a response to moisture gradient caused by a waterfall upstream. Individual habitat factors, although correlated with beetle assemblages, were not of great assistance for explaining species distributions. The findings do suggest that specific site conditions can influence ground-dwelling beetles, and the general riparian response cannot be expected to hold true for all first order streams. Our results also showed a trend in support of the hypothesis of greater diversity between positions along streams compared to diversity in upslope communities. Forest conservation efforts and placement of reserves to protect terrestrial species should not necessarily be focused on the riparian zone in preference to upslope areas.

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Chapter 4

Why conservation reserves should not always be concentrated in riparian areas: a study of ground-dwelling beetles in wet eucalypt forest

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Preface: This chapter documents the abundance and diversity of beetles over the riparian-upslope transition in mature forest.

Abstract

Reserve corridors in production forestry landscapes are frequently concentrated in riparian areas. This study describes the numerical response of ground-dwelling beetles to increasing distance from streams, with the aim of evaluating the effectiveness of such a bias in reserve allocation. Patterns in abundance and diversity of epigaeic beetles were quantified at four first order streams in wet eucalypt forest in Tasmania, Australia. The depth and pattern of beetles' riparian response varied between streams. Commonly trapped beetles were less abundant near to three of the four streams, and the numerical response model differed in each case. Species richness of common beetles was also lower near one of the streams. Pooled abundance and richness of rare species did not vary in response to the riparian-upslope transition. No riparian or upslope specialist species were identified among the most commonly collected species. Compared to upslope habitat, the riparian-upslope transition encompassed greater variability in species composition without actually increasing overall richness. The study findings demonstrate the need for ecosystem-specific data to optimize reserve placement, since the results were not predicted from general vegetation patterns, ecological theory, or the widely held assumption that riparian areas support greater abundance and diversity of organisms than adjacent upslope areas. Reserves encompassing more upslope habitat are recommended to complement those located in riparian areas.

Keywords: upslope habitat, headwater streams, clearcut logging, abundance, species richness, species turnover

Introduction

In production forestry landscapes, careful consideration needs to be given to the design and placement of reserves between logging coupes. Streamside buffers are a common requirement of legislation governing forest practices worldwide (Westland Resource Group, 1995). In Tasmania, Australia, the reserve corridor network is largely composed of streamside reserves consisting of $\geq 20\text{--}30$ m wide strips of uncut forest adjacent to streams of catchment area exceeding 50 hectares (Forest Practices Board, 2000). Additionally, 100 m wide wildlife habitat strips are located every 3–5 km in the landscape; these are mostly aligned as widened streamside reserves, but include some linkages up slopes and across ridges (Forest Practices Board, 2000). Along with local reserves, the network of streamside reserves and wildlife habitat strips is intended to retain biodiversity at the landscape level (Forestry Tasmania, 2004). There are potential advantages and disadvantages of a largely riparian-aligned reserve system. If, as is often supposed (Naiman et al., 1993; Araujo, 2002; Kati et al., 2004), abundance and diversity of animals and plants is higher in riparian areas, then this positioning could maximise the benefits per unit reserve area. But if this is not the case, or if certain species are riparian-avoiding, then more equitable reserve allocation between upslope and riparian habitats may be more appropriate (Whitaker et al., 2000; Sabo et al., 2005).

As suggested by J.B.S. Haldane's famous comment on the Creator's "inordinate fondness for beetles", the Coleoptera are an exceptionally diverse and abundant group of terrestrial invertebrates (Grove and Stork, 2000). High local diversity and abundance of forest ground-dwelling (epigaeic) beetles arises from their taxonomic and trophic diversity and a high capacity for niche partitioning (Lawrence and Britton, 1994). Sensitivity to habitat conditions also means that beetles respond to

natural environmental gradients and human induced habitat changes such as logging (Brenner, 2000; Taylor et al., 2000; Dangerfield et al., 2003). The riparian-upslope transition is a common natural environmental gradient in wet forest areas. First order streams are prevalent in the landscape compared to higher order streams, and are commonly buffered under forest practices legislation (Forest Practices Board, 2000). The objective of this study is to document the numerical response of ground-dwelling beetles to riparian areas adjacent to small streams, in order to assess the effectiveness of a largely riparian-aligned reserve system. The degree to which riparian patterns in species diversity can be predicted by ecological theory, or by patterns observed in other systems, is also of interest.

Several alternative hypotheses might predict the numerical response of ground-dwelling beetles to riparian areas in wet eucalypt forest. Beetles may be predicted to be of greatest abundance and diversity in riparian compared to upslope habitat. Like many plants and animals, beetles have been found in several studies to be more numerous and diverse in riparian than upslope areas (Brenner, 2000; Catterall et al., 2001; Davis et al., 2001; Hutchens and Wallace, 2002; Gutierrez et al., 2004). Elevated soil moisture (Niemelä et al., 1992) or greater small-scale habitat heterogeneity (Niemelä et al., 1996), and the potential for a wider variety of food resources (Brenner, 2000), could result in greater species diversity in riparian areas, especially those subject to occasional disturbance (Gregory et al., 1991; Naiman and Décamps, 1997). Presence of riparian-specialist beetle species may also elevate species diversity; e.g. species with aquatic larval but terrestrial adult life histories, or terrestrial predators specialised to feed on aquatic invertebrate prey. However, increased diversity in riparian areas is not universal (Sabo et al., 2005), varying between species and ecosystems, with some beetle species usually preferring upslope to riparian habitat (Brenner, 2000; Davis et al., 2001).

Several mechanisms could potentially result in diversity and abundance peaking at intermediate distances from streams. Relatively high proportions of natural edges between adjacent riparian and upslope communities characterize riparian areas (Naiman et al., 1988; Hewitt, 1990), suggesting the possibility of a riparian “edge effect” of elevated abundance and richness at the interface between riparian and upslope habitats (birds, Gates and Giffen, 1991; LaRue et al., 1995). In this ecosystem, the riparian-upslope interface would more likely be a “soft” edge (Ries et al., 2004) or ecotone, in contrast to “hard” edges between highly contrasting environments (e.g. environments with obvious vegetative riparian strips). The riparian-upslope transition may represent a natural productivity (e.g. nutrients, moisture, temperature, light) gradient or a disturbance gradient arising from occasional flooding of the riparian area nearest the stream. Greatest diversity at some intermediate level of disturbance and/or productivity, i.e. at some point upslope from the stream, might therefore be predicted based on the intermediate disturbance hypothesis (Connell, 1978), the intermediate productivity hypothesis (Grime, 1973) or the dynamic equilibrium model (a synthesis of the previous two models, Huston, 1979,1994).

Based on general vegetation patterns, beetle abundance and diversity in this forest type may be predicted to be unrelated to distance from streams. General vegetation patterns are often used as a basis to allocate reserves, with the implicit assumption that vegetation is an effective surrogate for other taxa (Oliver et al., 1998). Unlike in drier forests, obvious riparian vegetation bands do not fringe streams in wet *Eucalyptus obliqua* forests. Therefore, if vegetation can be regarded as a surrogate, beetles may not respond to riparian areas in this forest type.

Species turnover and accumulated species richness may be higher in areas that encompass both riparian and upslope habitat (Sabo et al., 2005). If different species

use riparian and upslope habitats then more equitable allocation of reserves to these two landscapes is warranted (McGarigal and McComb, 1992; Whitaker and Montevecchi, 1999). For example, Taylor et al. (1994) identified a species of land snail from drier forests in north-eastern Tasmania which they considered would not be adequately reserved by streamside reserves because of its habitat requirements for drier areas upslope. Conversely, Brenner (2000) collected more rare beetle species in riparian than upslope forest in Oregon. Rare species may have more specialised habitat requirements, and therefore be more sensitive to conditions along the riparian-upslope gradient, than common species. The response of beetles to riparian-upslope gradients might also be site-specific. This may result from differences in the physical characteristics of riparian areas between streams, and from beetle assemblage turnover between catchments (Baker et al., 2004).

This study examines the nature and scale of the response of terrestrial ground-dwelling beetles to small streams in wet eucalypt forest. An understanding of the nature and extent of riparian influences is relevant to determining the width and landscape position of reserve corridors that will be effective in conserving habitat for both riparian and non-riparian species. The following hypotheses are tested:

1. Beetles will
 - (a) be more abundant and of higher species richness closer to the streams; or
 - (b) be more abundant and of higher species richness at an intermediate zone upslope from the streams; or
 - (c) not vary with distance from streams.
2. (a) Species turnover in beetles will be greater over the riparian-upslope transition than over the same scale in non-riparian habitat away from streams.
- (b) Accumulated species richness will be greater in riparian-upslope transects than upslope-only transects.

3. Some beetle species will show preferences for riparian or upslope conditions.
4. Riparian response will be site-specific.
5. As a group, rare beetles will be more responsive than common beetles to riparian influences.

Methods

Study area

Beetles were sampled adjacent to four streams and nearby upslope forest in southern Tasmania, Australia, where annual rainfall is about 1300 mm. Streams were located in mature ‘wet’ *Eucalyptus obliqua* forest with a mixed understorey of rainforest and sclerophyllous species (Neyland, 2001). Tall, wet eucalypt forests are highly productive sources of hardwood timber in Tasmania; they have been harvested since the 1960s with clearcut harvesting of 50 ha. coupes (average) on a nominal 90 year rotation (Forestry Tasmania, 1998; Hickey and Neyland, 2000; Hickey et al., 2001); however, in the future some aggregated retention harvesting (Hickey et al., 2001) will also be used. Unlike drier forest communities, the vegetation in the riparian zone did not appear to be delineated from upslope forest. However, a detailed botanical survey was not conducted. The four study streams were small-sized perennial first order streams representative of the ranges of size, channel morphology, and bank slopes of streams that would be reserved under the Forest Practices Code (Forest Practices Board, 2000). The streams were King Creek (Warra area), Isabel Creek (Picton area), Leas Creek (Manuka Rd area), and Critter Creek (Kermandie area). More details about the study sites, including stream widths and stream and bank slopes are given elsewhere (Chapter 3). Isabel Creek was the biggest stream and had a 10 m high waterfall 35 m upstream of the closest study transect. Isabel and King

Creeks were wider than Leas and Critter Creeks, had greater water flow, and much steeper stream banks. Leas Creek and Critter Creek flowed underground for part of their courses, particularly the multi-channelled Leas Creek, which was occasionally visible where a sedimentary outcrop forced water to the surface. Occasional flooding of streams during peak flow conditions could disturb the adjacent habitat for 1-2 m at these sites (personal observation).

Study design and beetle sampling

At each site (stream), three replicate transects of pitfall traps were established at right angles to the stream channel (riparian-upslope transects). An additional three transects were randomly positioned in nearby forest >100 m from streams (upslope-only transects, see Chapter 2). Transects were randomly positioned, but located at least 100 m from roads or logging coupes to avoid confounding by edge effects. Adjacent transects were separated by at least 25 m. All riparian transects were located at positions where streams flowed above ground. Beetles were collected using pitfall traps; a single pitfall trap was located at 1 m, 5 m, 10 m, 25 m, 50 m and 100 m from the stream in each riparian-upslope transect, and for upslope-only transects, pitfall traps were located the same distances apart on a random bearing from a random starting point. Unlike many studies where riparian and upslope habitats were defined a priori from vegetation characteristics (Brenner, 2000; Everett et al., 2003), this study was designed to define the riparian zone based on emergent patterns observed in the distribution of the beetles. The design assumes that the transition from riparian to upslope habitat for small streams in wet forest would occur within the first 100 m from streams.

Collecting samples at unequal distances within transects is a design commonly employed in studies of environmental gradients such as edge effects (e.g. Bedford

and Usher, 1994; Didham et al., 1998; Kotze and Samways, 2001; Dangerfield et al., 2003) since it concentrates sampling effort in the region where change is considered most likely. However, this design risks confounding patterns in diversity and abundance with patterns attributable to spatial autocorrelation or pitfall trap depletion, such that reduced abundance or species richness of beetles could be recorded from more closely positioned pitfall traps. In order to rule out these confounding influences, data from upslope-only transects were tested. Depletion and autocorrelation were demonstrated to not be a significant influence on pitfall catches of beetles in this forest type (Chapter 2).

Pitfall traps are the most widely used collection method for ground-dwelling beetles (Gandhi et al., 2001; Ward et al., 2001; Davies et al., 2004; de Warnaffe and Lebrun, 2004). It is important to recognise that pitfall trapping has some inherent biases, and catches can be affected by factors including habitat structure, weather and the preservative used (Greenslade, 1964; Spence and Niemelä, 1994; Melbourne, 1999). However, standardized concurrent pitfall trapping is an appropriate collection method in this study, since the intention was to make comparisons of relative beetle abundance and species richness within the riparian-upslope transition. Because pitfall trapping may not necessarily trap all species present in an area, and trapping efficiency will vary between species depending on their activity and other behavior, abundance estimates are actually a measure of ‘activity-abundance’, and species richness estimates will be underestimates of the true number of species (Thiele, 1977; Niemelä et al., 1993; Fisher, 1999). Combined use of pitfall sampling and litter extraction would possibly have yielded a more complete species inventory (Fisher, 1999; York, 1999; Rieske and Buss, 2001).

Traps were operated continuously during three separate one-month periods: winter (June – July 2001), spring (October – November 2001) and summer/autumn

(February – March 2002). These periods were spaced four months apart over a twelve-month period in order to encompass seasonality in beetle activity. The hypothesis was tested that seasonal variation was not important in structuring the response of beetles to distance from the streams (Chapter 3). Data from the three trapping periods were pooled after ascertaining that beetles were not shifting up- or down-slope at different times of the year (Chapter 3). Exploring seasonal patterns was not an objective of this study, and pooling data from the trapping periods provided a more robust dataset for statistical analyses. The pitfall traps consisted of 225 mL plastic cups suspended in PVC downpipe sleeves (7.5 cm external diameter, 10 cm deep). The cups were filled to 4 cm depth with ethylene glycol as a preservative. A 12 cm diameter plastic lid was supported approximately 3 cm above each trap with three wooden sticks to protect the traps from disturbance by vertebrates and rain.

Beetles were sorted to family and morphospecies based on external morphology, using the protocols of Oliver and Beattie (1996) and keys to family in Lawrence and Britton (1994) and Lawrence et al. (1999). Taxonomic knowledge of many beetle families is scarce, and identification to taxonomic species was not possible for all morphospecies. Species identifications were made by reference to the Tasmanian Forest Insect Collection at Forestry Tasmania, where the reference collection will be deposited.

Statistical Analysis

Most of the analyses tested patterns in riparian response using the riparian-upslope transects. The statistical package R Version 1.8.1 (R Development Core Team, 2003) was used to test for variation in abundance (total, common species and rare species) and diversity (species richness and Margalef diversity (Magurran, 2004)) in relation

to the different study sites and distances from streams (both fixed factors). Rare species were defined as those species having abundance less than 0.5% of the total abundance, or that were recorded only from single samples; other species were defined as common. The data for several variables did not conform to a Gaussian distribution, preventing the use of standard linear regression and ANOVA techniques. Instead, generalized linear models were adopted for analysis of multi-species abundance and diversity variables. Only the abundance of the single most common individual species, *Aleoc_1* (Staphylinidae: Aleocharinae) ($n = 408$ across all sites) could be tested with generalized linear models; some other individual species were tested with the zero-inflated Poisson model (below). Checking model dispersion, and the normal quartile and residuals plots, identified whether a variable best fitted a Poisson, negative binomial, or Gaussian error distribution (Crawley, 2003). Model simplification followed the approach recommended in Crawley (2003). The percentage variance explained by each factor was calculated from changes in model deviance compared to the null model. When a significant interaction ($P < 0.05$) was found between study sites and distance from stream, distance effects were further explored on a site-by-site basis.

If the distance from stream had a significant effect on beetle response, a post hoc analysis was carried out to test the relationship between distance from stream and beetle response. Several alternative models were assessed, with the best fitting model selected as describing the relationship between distance from stream and beetle response. Eight different models for the response of beetles to distance from stream were compared (Table 1).

Table 1 - Description of eight alternative models for the relationship between beetle response variables and distance from stream.

Model	Hypothesis tested	Treatment of distance from stream	Description
1	1a	Distance categories are a linear covariate	Beetle response decays with distance from stream
2	1a	Distance from stream (m) is a linear covariate	Beetle response varies linearly with distance from stream
3	1a	1 m vs. ≥ 5 m	The riparian zone for beetle response is within 5 m of the stream
4	1a	≤ 5 m vs. > 10 m	The riparian zone for beetle response is within 10 m of the stream
5	1a, 1b	1 m vs. 5 m vs. ≥ 10 m	There is an intermediate zone for beetles between the riparian and upslope zones
6	1a, 1b	Distance categories are a quadratic covariate	There is a quadratic relationship that decays with distance from stream
7	1a, 1b	Distance from stream (m) is a quadratic covariate	The beetle response is quadratic with distance from stream
8	1c	Factor	There is no discernable pattern between beetle response and distance from stream

To model a decaying effect of distance from stream on the beetle response, as represented by the increasing distance between pitfall traps away from the stream, distance categories were treated as a linear covariate in some models. “Decaying effect” means that the effect of distance from stream on beetle response variables gets weaker as distance increases. The Bayesian Information Criterion was used to select the model which best fitted the riparian response type for each beetle response variable (Crawley, 2003; Maindonald and Braun, 2003). The Bayesian Information Criterion is a relative value; when comparing several models, the smaller the value, the better the fit (Crawley, 2003). The Bayesian Information Criterion is similar to the Akaike Information Criterion, but penalises models with many parameters more strongly, and is less likely to result in overfitting (Maindonald and Braun, 2003). The model error distributions found to best fit the data during significance testing were also used for response type comparisons.

The riparian responses of the most abundant individual beetle species were analysed using the zero-inflated Poisson model with the Zicounts package (Mwalili, 2005) in R, since zero-inflation precluded use of generalized linear models. The zero-inflated Poisson model combines Poisson and zero-inflated components to model count data (Cheung, 2002; Lewsey and Thomson, 2004). Initially a factorial model across all sites was used to test site and distance from stream effects on beetles. If this identified a significant interaction between main factor effects, then site-specific analyses were conducted using a zero-inflated Poisson linear model in which distance from stream was treated as a linear covariate. Since there was insufficient power with three transects to treat distance from stream as a quadratic covariate, significance of the Poisson component of these analyses indicates that beetle abundance either increased or decreased with distance from the stream.

Significance of the zero-inflated component indicates that the likelihood of beetle presence changed with the distance from the stream.

Species turnover and accumulated species richness were compared between the riparian-upslope transects and the upslope-only transects. Species turnover was calculated between the traps positioned at 1 m and 100 m (i.e. 99 m apart) for each transect using the Marczewski-Steinhaus distance, which is the complement of the Jaccard similarity index (Magurran, 2004; Sabo et al., 2005). Accumulated species richness was the total number of species collected from all six traps for each transect. Factorial ANOVA was used to test for differences in turnover and accumulated richness between habitats and between study sites.

Results

In total, 2,021 beetles were trapped in riparian-upslope transects, representing 173 morphospecies from 26 families. Abundance and richness of beetles varied between sites and distances from streams (Table 2). Overall abundance (N total) was lowest close to Isabel (Fig. 1A), King (Fig. 2A) and Critter Creeks (n.s. at Critter Creek), a result probably driven by the abundance of common beetles, which was also significantly lower close to these three streams than further upslope (Fig. 1B, 2B and 3A). The overall abundance and species richness of rarely trapped beetles did not differ significantly with distance from streams. The riparian zone had less influence on species richness than abundance of beetles; species richness of common beetles was lower close to King Creek than upslope (Fig. 2C). Margalef diversity (Magurran, 2004) was unaffected by riparian influences.

Table 2 - Summary of generalized linear modeling results of beetle abundance, species richness and Margalef diversity.

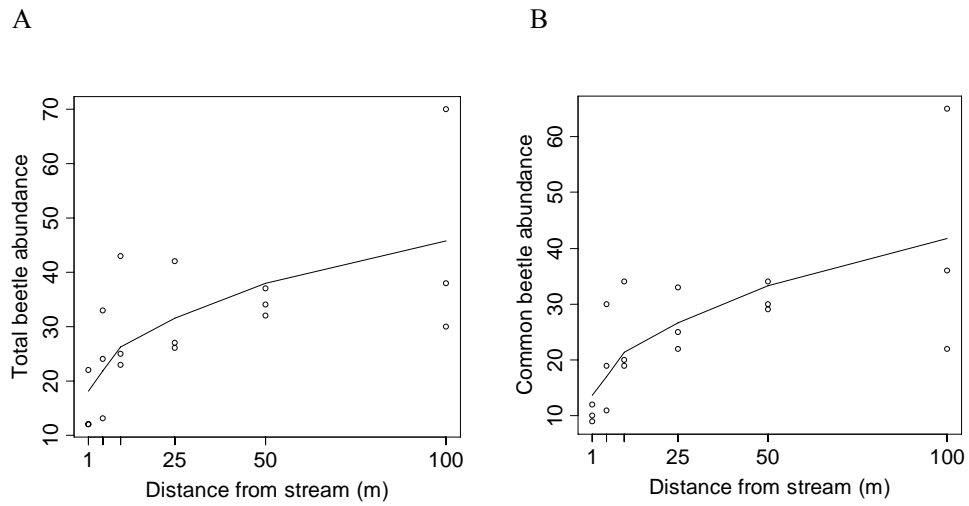
Diversity Index	Model	% Variance explained		Mean abundance at each site					Mean value at each distance from stream					
		Site	Distance	Distance	Isabel	King	Leas	Critter	1 m	5 m	10 m	25 m	50 m	100 m
N – total	NB	36.6	16.1	17.7*										
- Isabel Creek	NB		57.1*						15.3	23.3	30.3	31.7	34.3	46.0
- King Creek	NB		82.8*						10.0	24.7	23.0	15.7	18.7	47.0
- Leas Creek	NB		26.0						18.0	20.7	11.3	20.3	12.7	12.3
- Critter Creek	NB		42.8						19.3	39.7	45.0	51.7	51.7	51.0
N – common species	NB	28.1	18.7	21.5*										
- Isabel Creek	NB		65.3*						10.3	20.0	24.3	26.7	31.0	41.0
- King Creek	NB		81.6*						6.0	20.7	20.3	12.7	17.7	39.7
- Leas Creek	NB		31.1						16.0	18.0	8.0	19.0	10.7	9.7
- Critter Creek	NB		45.0*						13.0	29.7	40.0	39.3	42.7	43.3
N – rare species	NB	39.1*	3.5	16.6	4.6	3.7	2.3	8.4	4.3	5.0	4.3	5.4	3.8	5.7
S – total	P	46.1*	7.9	14.3	12.5	11.4	8.7	17.8	9.8	12.7	13.3	13.7	13.1	13.3
S – common species	G	21.4	16.7	28.5*										
- Isabel Creek	P		48.3						5.3	7.7	8.3	9.3	12.0	10.0
- King Creek	G (ln)		76.1*						3.3	7.0	12.0	7.3	9.7	10.7
- Leas Creek	G (^2)		37.3						7.0	8.7	5.0	7.7	6.0	5.0
- Critter Creek	P		62.8						7.7	10.3	12.7	13.7	10.0	9.7
S – rare species	P	45.8*	1.0	13.4	3.7	3.1	2.2	7.2	3.9	4.3	3.8	4.2	3.7	4.4
Margalef diversity	G	38.1*	3.4	15.0	3.5	3.4	2.9	4.6	3.3	3.6	3.8	3.8	3.6	3.4
N – Staphylinidae, Aleocharinae: Aleoc_1	NB	29.7	4.3	21.4*										
- Isabel Creek	NB		0.5						5.3	8.3	9.0	11.0	7.3	7.0
- King Creek	NB		4.3						2.3	4.0	0.3	2.0	2.7	6.0
- Leas Creek	NB		3.4						3.7	2.3	0.7	10.	0.3	2.7
- Critter Creek	P		32.5*						0.3	6.7	11.7	8.0	14.3	19.0

Notes: Significance: * indicates statistical significance (P<0.05). Site-based results are presented when the site x distance interaction is significant. Model type: G, gaussian; P, poisson; NB, negative binomial; ln, natural log transformation; ^2, power transformation.

Table 3 - Model comparisons for the response of ground-dwelling beetles to distance from streams. Descriptions of the eight models are given in Table 1. Lower Bayesian Information Criterion values indicate better model fit. The relative order of explanatory value for each model is indicated in superscript with the Bayesian Information Criterion value, and the best model for each dataset is indicated in bold type.

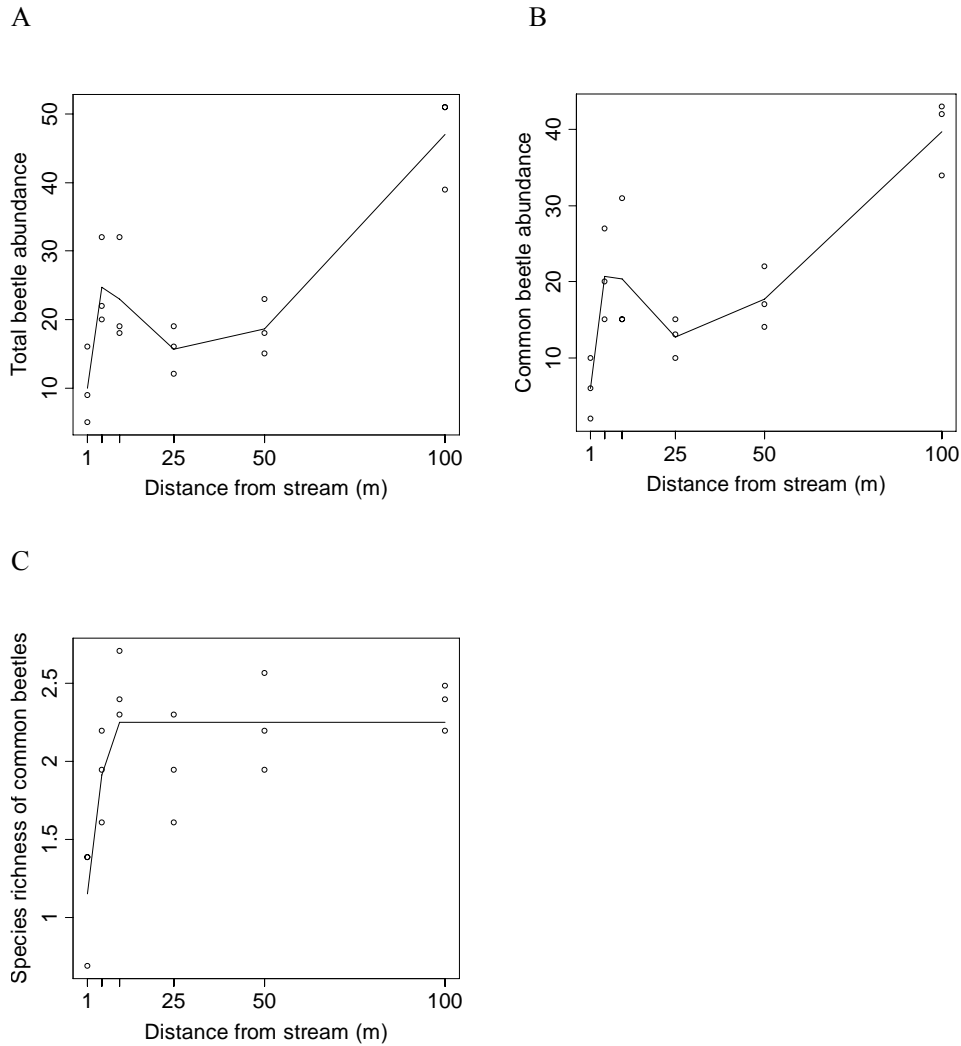
Diversity Index	Bayesian Information Criterion							
	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6	Model 7	Model 8
N – total at Isabel Ck.	133.68¹	137.78 ⁴	139.12 ⁶	137.70 ³	138.50 ⁵	136.02 ²	139.29 ⁷	143.25 ⁸
N – common at Isabel Ck.	128.71¹	134.17 ⁵	134.04 ⁴	134.91 ⁷	133.71 ³	130.60 ²	134.83 ⁶	137.24 ⁸
N – total at King Ck.	135.06 ⁴	132.53 ²	136.51 ⁵	141.45 ⁸	139.36 ⁷	137.45 ⁶	132.79 ³	124.44¹
N – common at King Ck.	131.81 ⁴	131.32 ³	130.58 ²	138.10 ⁸	133.38 ⁵	134.70 ⁷	133.50 ⁶	121.80¹
S – common at King Ck.	22.40 ⁶	17.48 ⁷	15.22 ²	27.45 ⁵	15.12¹	20.23 ⁴	20.44 ⁸	17.48 ³
N – common at Critter Ck.	153.30 ⁵	156.86 ⁶	149.69¹	153.01 ⁴	151.14 ²	152.32 ³	157.47 ⁷	159.68 ⁸
Aleoc_1 at Critter Ck.	181.92 ⁵	197.23 ⁸	181.71 ⁴	192.79 ⁶	174.61 ²	179.86 ³	193.61 ⁷	168.56¹

Fig. 1 - Beetle abundance at Isabel Creek; A) total abundance (Model 1) and B) common species abundance (Model 1). The points indicate data from the three transects, and lines represent the fitted riparian response models.



The best fitting riparian response functions (Table 3) were in three cases random (Model 8), in two cases decaying curvilinear (Model 1), in one case indicative of a < 5 m riparian zone (Model 3), and in one case indicative of an intermediate zone at 5 m between riparian and upslope zones (Model 5), with no evidence of abundance or richness measures following a quadratic response to riparian influences. Total abundance appeared to be closely related to common beetle abundance at Isabel (Fig. 1) and King (Fig. 2A, B) Creeks. The total and common beetle abundance response functions at Isabel Creek showed a decaying curvilinear pattern of increasing abundance with distance from stream such that abundance at 100 m was more than double that at 1 m from the stream (Model 1, Fig. 1).

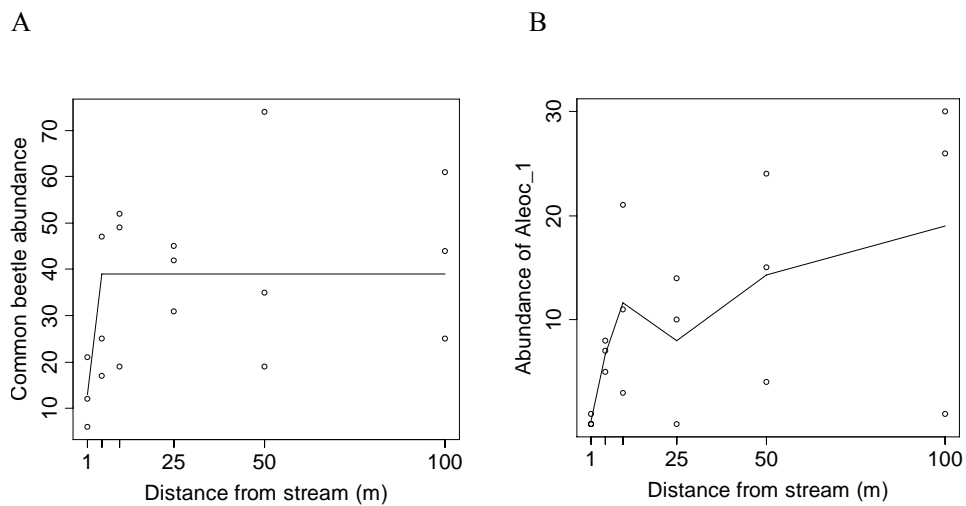
Fig. 2 - Beetle abundance and richness at King Creek; A) total abundance (Model 8), B) common species abundance (Model 8), and C) common beetle species richness (Model 6). The points indicate data from the three transects, and lines represent the fitted riparian response models.



Total and common beetle abundance best fitted the random model (Model 8, Fig. 2A, B) at King Creek, as did the abundance of the staphylinid *Aleoc_1* at Critter Creek (Fig. 3B), although abundances in each case were lowest at 1 m from to the stream. Common beetle species richness at King Creek best fitted Model 5 (Fig. 2C), with lowest richness at 1 m, intermediate richness at 5 m and constant higher richness from 10 m to 100 m upslope. Upslope richness was approximately double that at 1 m. Abundance of common beetles at Critter Creek also was indicative of a <5 m riparian zone (Model 3, Fig. 3A); abundance at 1 m from stream was less than half

that further upslope. All abundance and richness measures differed between study sites (Table 2), and were greatest at the Critter Creek site followed by Isabel Creek, then King Creek, with fewest beetles and species at Leas Creek.

Fig. 3 - Beetle abundance at Critter Creek; A) common species abundance (Model 3), and B) the abundance of *Aleoec_1* (Model 8). The points indicate data from the three transects, and lines represent the fitted riparian response models.



No consistent trends were apparent in the riparian responses of other individual beetle species (Table 4). With the exception of *Decilaus nigronotatus* (Curculionidae), riparian responses were found to differ between study sites. Although significant relationships with distance from stream were generally in the form of increasing abundance upslope, the inconsistency between study sites, and the presence of each species in some plots 1 m from streams, suggest that these species are not upslope specialists. No riparian specialists were evident among the common species, since none were more abundant near streams.

Species turnover within 99 m transects was approximately 10% greater in the riparian-upslope transects compared to upslope-only transects (Table 5).

Significantly greater turnover was also found between 5 m and 100 m traps in transects (results not presented). Accumulated species richness did not vary between riparian-upslope and upslope-only landscape positions, although it did differ between sites (Table 5). The riparian-upslope transition zone thus appeared to have more varied species composition than upslope areas, without harbouring more species.

Discussion

Effects of riparian-upslope transition on litter beetles

The response of ground-dwelling beetles to riparian areas was unexpected, and patterns of abundance and species richness did not conform to the a priori hypotheses based on general vegetation patterns, ecological theory, or the widely held assumption that riparian areas support greater abundance and diversity of organisms than adjacent upslope areas. The response of beetles varied from stream to stream, but fewer beetles, especially of common species, were collected close to three of the four streams, and species richness was lower near one stream. The abundance and diversity of beetles were not affected by riparian influences at the smallest stream, Leas Creek. Common individual species were found to be generalists, and the riparian-upslope transition zone did not support a greater number of species than upslope habitat.

Table 4 - Summary results from zero-inflated Poisson analysis of responses of common morphospecies to site and distance from stream (Dist).

<i>Morphospecies</i>	N	Likelihood Ratio – Poisson			Likelihood Ratio – Zero Inflated			Mean abundance at each distance from stream						
		Site	Dist.	Site x Dist.	Site	Dist.	Site x Dist.	1 m	5 m	10 m	25 m	50 m	100 m	
Carabidae:														
<i>Rhabdotus reflexus</i>	99			41.98*	0.88	5.04	25.15							
- Isabel Creek	42		4.55*			11.67*		0.00	0.67	1.00	3.33	4.00	5.00	
- King Creek	6		0.34			0.13		0.00	0.33	1.33	0.00	0.00	0.33	
- Leas Creek	1		-			-		0.00	0.00	0.00	0.00	0.00	0.33	
- Critter Creek	50		0.14			0.46		1.67	3.33	4.00	0.67	6.67	0.33	
Leiodidae: Cholevinae														
<i>Choleva</i> TFIC sp. 01	75			26.6*			13.3							
- Isabel Creek	24		0.04			2.45		0.33	0.00	0.00	3.00	2.67	2.00	
- King Creek	14		11.42*			1.24		0.00	0.33	0.67	0.00	0.67	3.00	
- Leas Creek	33		0.59			0.04		0.33	3.67	0.00	2.33	2.33	2.33	
- Critter Creek	4		-			-		0.33	0.00	0.33	0.00	0.33	0.33	
Leiodidae: Cholevinae														
<i>Austronemadus</i> TFIC sp 03	161			31.96*			24.08							
- Isabel Creek	11		0.004			3.03		0.33	1.00	0.00	0.33	1.17	0.33	
- King Creek	51		6.11*			0.09		0.33	4.00	0.67	3.33	4.00	4.67	
- Leas Creek	12		1.57			1.80		1.33	1.00	0.00	1.67	0.00	0.00	
- Critter Creek	87		12.67*			1.35		2.00	1.00	4.67	1.00	11.00	9.33	
Curculionidae:														
Cryptorhynchinae														
<i>Decilaus nigrnotatus</i>	51	7.1	11.7*	14.1	3.8	6.5	9.1	0.25	0.67	1.08	1.42	0.58	0.25	

		Likelihood Ratio – Poisson	Likelihood Ratio – Zero Inflated	Mean abundance at each distance from stream						
Curculionidae:										
Cryptorhynchinae										
<i>Decilaus striatus</i>	73	36.51*	23.17							
- Isabel Creek	22	0.66	1.37	0.67	2.00	2.67	0.67	0.67	0.67	
- King Creek	11	0.93	1.04	0.67	0.33	2.00	0.00	0.67	0.00	
- Leas Creek	7	-	-	0.67	1.00	0.33	0.00	0.00	0.33	
- Critter Creek	33	14.68*	2.97	0.33	0.00	1.00	4.00	2.00	3.67	
Curculionidae:										
Cryptorhynchinae										
<i>Roptoperus tasmaniensis</i>	62	29.64*	16.87							
- Isabel Creek	19	8.56*	0.78	1.00	1.67	2.67	0.67	0.33	0.00	
- King Creek	15	5.51*	0.88	0.00	0.67	0.67	0.00	2.00	1.67	
- Leas Creek	15	0.70	1.73	1.00	1.33	0.00	1.33	1.33	0.00	
- Critter Creek	13	0.35	0.43	0.00	0.33	1.33	1.00	1.33	0.33	

Notes: Significance: * indicates statistical significance (P<0.05). Site-based results are presented when the site x distance interaction is significant. “-” indicates that insufficient non-zero data were available for zero-inflated Poisson analysis.

Table 5 - Summary of ANOVA results comparing species turnover and accumulated species richness between riparian-upslope and upslope-only transects.

Variable	Site		Habitat		Site x Habitat		Residual	Mean ± 1 SE	
	MS	F	MS	F	MS	F	MS	Riparian	Upslope
Species Turnover (%)	0.0027	0.8673	0.0613	19.64*	0.0038	1.220	0.0031	90.9 ± 1.7	80.8 ± 1.6
Accumulated S	619.0	19.47*	0.0400	0.0013	59.04	1.857	31.79	46.0 ± 3.2	46.1 ± 3.0

Notes: Significance: * indicates statistical significance (P<0.05).
d.f.: Site = 3, Habitat = 1, Site x Habitat = 3, Residuals = 16.

These results illustrate a situation where beetles were less abundant and diverse in the riparian zone; and thus were not consistent with the widespread notion that riparian areas are havens of high diversity and numbers of animals (Gregory et al., 1991; Catterall, 1993; Pollock, 1998; Naiman et al., 2000); although it should be noted that Sabo et al.'s (2005) multi-taxon meta analysis demonstrated that riparian areas are not necessarily more diverse than upland areas. Lower abundance or richness in riparian compared to upslope areas has been occasionally recorded, although only for birds (McGarigal and McComb, 1992) and plants (Kirkman et al., 1998; Burnham, 2002; Schade et al., 2003). Yet, for invertebrates to be less abundant in the riparian zone is, to our knowledge, unprecedented (Janzen and Schoener, 1968; Brenner, 2000; Catterall et al., 2001; Davis et al., 2001; Hutchens and Wallace, 2002), but possibly relates to the wet forest context of this study where upslope conditions are apparently not limiting.

The role of riparian habitat, including characteristics such as moisture gradients, the presence of free water, and vegetation factors, probably increases in importance with the aridity of an area (McGarigal and McComb, 1992; Williams, 1994). For example, Meggs and Munks (2003) recorded the threatened Tasmanian lucanid beetle *Lissotes latidens* in damp and wet eucalypt forest away from streams, but only from the wetter riparian zones in dry forest areas. There was no evidence to suggest that abundance or diversity of beetles peaked at an intermediate distance upslope. Gradients in disturbance or productivity are likely to be considerably weaker in wet forest than more arid environments, and riparian 'edge effects' may be unlikely to occur in the absence of sharp vegetation boundaries. Another explanation may be that the 99 m transects were not long enough to encompass the ecological gradients fully, and thus detect a peak at intermediate levels. The adequacy of vegetation type as a surrogate for invertebrate communities is variable (Oliver et al., 1998; Panzer

and Schwartz, 1998; Mac Nally et al., 2002). Ground-dwelling beetles respond to various habitat characteristics (Greenslade, 1968; Szyszko, 1974; Thiele, 1977; McCracken, 1994; Humphrey et al., 1999), and factors other than general vegetation patterns appear to be related to the riparian response of beetles recorded in this study.

Riparian influences in this study generally affected beetle abundance to a greater degree than species richness, which was significantly greater upslope only at King Creek. The response model shapes for the abundance of common species differed between the three sites where a riparian response was recorded. However, all models illustrate lower abundance right at the stream edge (1 m from streams). This area is probably subject to occasional disturbance by flooding, potentially causing mortality of beetles or washing away leaf litter habitat, whereas forest 5 m and further upslope would be unaffected. At Isabel and King Creeks, the response models for total abundance were very similar to those for the abundance of common species, indicating that common species were driving the results for total abundance. At King Creek, the best fitting models for abundance had no consistent pattern, but abundance was lowest 1 m from the stream, and approximately four times greater 100 m upslope. The model for total species richness at this site had lowest richness 1 m from the stream, and intermediate richness at 5 m, indicating that richness was acting independently of abundance in this case. Unsurprisingly, riparian influences were greatest at the biggest stream, Isabel Creek, where abundance increased over the entire transect lengths. Similar results were found in analyses of multi-species beetle assemblages from the same dataset (Chapter 3).

Further research would be required to determine the mechanisms causing reduced beetle abundance near streams. Aquatic beetles were extremely rare in pitfall samples (Chapter 3), and no riparian specialist species were identified among the most common species, suggesting that riparian processes are not acting to increase

local diversity of beetles in this system, and other processes are enhancing habitat value further upslope. The trend for wider riparian-affected zones to be associated with bigger streams suggests factors related to site topography and stream size might be relevant, e.g. cold air drainage and gully flow (Mahrt et al., 2001), moisture and nutrient gradients, and the frequency and severity of flooding disturbance (Naiman et al., 2005). Elevated humidity caused by the waterfall at Isabel Creek might explain the stronger riparian response at that site. Riparian-affected areas may also have greater numbers of predators (e.g. invertebrates, birds) or subtle vegetation differences affecting quality and quantity of leaf litter.

Another possible explanation for lower abundance near streams is that the streams act as barriers to beetle movement, and could reduce pitfall trap catches because fewer beetles would be approaching from the streamward direction; although a ‘rebound effect’ (Lemieux and Lindgren, 2004) of beetles turning back after reaching the streams could counter this influence. As noted in the methods, pitfall trap depletion (Digweed et al., 1995), as a result of closer positioning of pitfall traps nearer the streams, was discarded as a possible explanation after testing beetle abundance data from upslope-only transects (Chapter 2). Other factors such as habitat complexity affect trappability (Greenslade, 1964; Melbourne, 1999), but habitat structural factors were weakly and inconsistently associated with beetle assemblages in this study (unpubl. data), and rare and common beetles should be equally affected.

In spite of the numerical dominance of rare species (approximately 80% of all beetle species collected), as a group they did not vary in abundance or number of species collected in relation to distance from streams. This result contrasts with those of Brenner’s (2000) riparian ground-dwelling beetle study and other studies that have found rare species to be more responsive than common ones (Faith and Norris, 1989;

Butterfield et al., 1995; Cao et al., 1998; Davies and Margules, 1998; Summerville and Crist, 2002). The explanation for why rare species in this study were unaffected overall when common species were less frequent next to streams is unclear. One possibility is that competition from more abundant and successful species is reduced near to the streams, compensating for an otherwise marginal habitat. Competitively dominant species may have poorer dispersal abilities (Didham et al., 1998) and thus avoid risky or marginal environments. Rare species can be associated with unusual or extreme environmental conditions (Kremen, 1992; Gaston, 1994), and it is possible that some rarely trapped beetles with riparian preferences balance numbers of those showing the more general response of avoiding this zone.

In contrast to the general findings of Sabo et al. (2005), riparian-upslope transition areas did not appear to have greater overall species richness than upslope-only areas, although variability in species patterns were greater in riparian areas. Disturbance possibly elevates local variability (Chapter 3), but from the same overall species pool.

Areas near to small streams in wet eucalypt forest, which do not have distinct riparian strips of vegetation, could be considered amongst the least likely of habitats to exhibit a riparian response. The findings that ground-dwelling beetles did in fact respond to this zone suggests that this group would probably also respond to riparian influences in most other environments. The unexpected finding of reduced abundance and richness near streams also illustrates that the riparian response of beetles, and presumably also certain other taxa, may not be predictable. More research into the mechanisms behind this observed response could provide general insights into the diversity patterning of beetles.

Relevance to reserve design

Riparian zones are often considered to have better habitat quality and, therefore, conservation value (but see Sabo et al. (2005)), but this does not appear to be so for ground-dwelling beetles at the streams investigated here. Reduced abundance of common species may actually indicate poorer habitat value immediately adjacent to streams, although this does not appear to be the case for rarely trapped species. Perhaps because the importance of riparian zones for wildlife habitat is such a widely accepted concept, there are very few published empirical studies relating to terrestrial invertebrates. The failure of ecological theory to predict the observed riparian response highlights the need for taxon- and ecosystem-specific research to guide reserve placement. Narrow streamside reserves may contain a significant proportion of riparian-affected habitat supporting relatively low numbers of ground-dwelling beetles, thus compromising to a certain extent their habitat value for terrestrial beetles. The results of this study suggest that reserves extending 100 m upslope should in most cases maintain equivalent species richness to upslope only habitat. However, the transition in abundance for the entire 100 m at Isabel Creek indicates that even wildlife habitat strips (see Introduction) may not fully encompass the riparian-upslope transition for some larger first order streams, and riparian-aligned reserves may not necessarily contain upslope habitat. Additionally, reserves encompassing the entire riparian-upslope transition have the potential to assist species' adaptation to future climate change (Araujo, 2002).

Whitaker et al. (2000) noted that conservation efforts in Canadian boreal forests, which also focus on the riparian zone, may not adequately protect certain species. Wildlife corridors incorporating more than one topographical position are recommended for conservation of arboreal marsupials (Lindenmayer et al., 1993; Lindenmayer and Nix, 1993). Since overall habitat quality appeared to be better

upslope for beetles, an emphasis on riparian zone conservation is probably not the best strategy for conservation of terrestrial invertebrates in this forest type. Whether certain rarely trapped species (which may be the most sensitive to habitat modification (Cao et al., 1998)) utilize both riparian and upslope habitats is more difficult to ascertain, and aligning reserves exclusively along streams (or upslope) would probably be unwise. Regardless, the tendency to concentrate most reserve corridors in Tasmania along riparian areas may not be optimal for beetle conservation. Unlike streamside reserves' primary role of protecting aquatic values, the function of wildlife habitat strips is the maintenance of terrestrial habitat. Location of a greater proportion of wildlife habitat strips upslope is recommended to enhance the reserve corridor network.

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Chapter 5

A comparison of litter beetle assemblages (Coleoptera) in mature and recently clearfelled *Eucalyptus obliqua* forest

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Preface: This chapter tests whether beetle assemblages differ between mature forest interior and young logging regeneration. It identifies indicator species for these forest ages that are used in the following thesis chapters.

Abstract

This study compares litter-dwelling beetles in mature wet eucalypt forest with those in young forest regenerated following clearfelling. The aims of the study were to determine the extent to which these forest ages support differing litter beetle assemblages, and to identify species characteristic of each age. Beetles were collected with pitfall traps in a spatially replicated study design to avoid confounding forest age and site differences. Three transects of traps were located in each of mature and young forest stands at four study sites. Beetle abundance was greatest in young forest, and young and mature forest supported distinctly different beetle assemblages. Of 37 commonly collected species, an indicator species analysis found 9 species characteristic of young logging regeneration, and 7 species characteristic of mature unlogged forest. These species could be useful in other Tasmanian studies concerning forest management impacts. Only two significant indicator species were carabids, suggesting that focusing only on carabids as indicators of forest management may be undesirable.

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Key words: Indicator species, habitat specialists, species assemblages, successional age

Introduction

Clearfell logging and the successional age of forest are two factors that are known to affect litter-inhabiting beetle populations (Niemelä *et al.* 1993; Michaels 1999). In Tasmania, recently harvested and regenerated clearfelled logging coupes differ substantially from mature forest with regards to stand structure, microclimate and vegetation composition (Westphalen 2003). Litter-dwelling Coleoptera (beetles) are known to respond to factors such as vegetation and microclimate and to conditions in the soil and litter layers; these are likely to vary between mature and recently regenerated forest (Greenslade 1968; Szyszko 1974; Niemelä *et al.* 1993).

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The effect of forest successional age on litter beetles in Tasmanian wet eucalypt forest have previously been investigated using a chronosequence approach (Michaels & McQuillan 1995; Michaels & Bornemissza 1999; Michaels 1999). Subsequent studies (Chapter 3, Baker *et al.* 2004) have found a high degree of litter beetle species turnover among sites. In this study we compare beetle assemblages in four spatially paired mature and recently harvested forest sites distributed over a broad area of forest, thereby removing confounding effects of geographic site separation from our investigation of how beetles respond to forest successional age.

An understanding of the effects of successional age and forest harvesting on beetles is important, since substantial areas of wet eucalypt forest are subject to logging, and these practices are changing the forest successional age structure compared to the natural situation in which forests regenerate periodically following wildfire (Baker *et al.* 2004). Beetles can be useful indicators, since they are sensitive to local and landscape scale habitat conditions, and thus also to forestry practices (Niemelä & Spence 1994; Niemelä 1997; Werner & Raffa 2000). Habitat preferences are not well understood for most Tasmanian invertebrate species. Indicator species of

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young and mature forest may be helpful in studies of the sustainability of current harvesting practices and alternative silvicultural approaches (Bashford *et al.* 2001; Hickey *et al.* 2001).

The aims of the study were to a) investigate forest age (young logging regeneration versus mature unlogged forest) and site effects on litter-dwelling beetle assemblage composition, abundance and species richness; b) identify species characteristic of young and mature forest.

Materials and Methods

Study sites

The study was conducted in the wet forests of southern Tasmania, approximately 60 km south-west of Hobart. The four study sites (Warra, Manuka, Kermadie and Picton, Table 1) were from 3 to 21 km distant from each other. Warra and Manuka sites are located within the Warra Long Term Ecological Research site (Brown *et al.* 2001). At each study site, sampling was conducted within a stand of recently clearfell logged and regenerated ‘young’ forest, and within adjacent unharvested ‘mature’ forest. This study forms part of a broader study into edge and riparian effects on forest litter beetles. Two mature forest stands adjacent to each recently harvested coupe were used (Table 1) so that representative control areas were provided for these other studies. The mature forest sites are advanced regeneration and old-growth forest resulting from previous wildfires, and dominated by *Eucalyptus obliqua* with some *E. regnans* and *E. delegatensis*, and mixed rainforest and sclerophyllous understoreys. Without detailed dendrochronological research, it is not possible to accurately estimate *E. obliqua* stand age based on tree heights and diameters (Alcorn *et al.* 2001); however the mature forest probably ranged in age from 1934 regrowth

to 300-400 year-old old-growth, with mosaics of several fire ages common (Hickey *et al.* 1998; Alcorn *et al.* 2001). Some selective logging may have occurred in these areas prior to the commencement of clearfell logging and stand record-keeping in the 1960's (Hickey *et al.* 2001). Since then, clearfell harvesting followed by a high intensity regeneration burn, nominally on 80-100 year rotations, has been the main silvicultural system in lowland Tasmanian wet eucalypt forest (Forestry Tasmania 1998). The young clearfell logging regeneration forest areas varied from 1-5 year old, and from low seedlings below 1 m height to dense cover of *E. obliqua* and understorey shrubs up to approximately 4 m height.

Table 1. Characteristics of the study sites. 'FT' refers to Forestry Tasmania, 'y' indicates young forest and 'm' indicates mature forest areas.

Site	Location	FT Coupe Number	Elevation	Dominant landform	Young forest - Regenerated
Picton	43° 7' S	PC024A (y)	150 m	Permian	2000
	146° 42' E	PC023D (m)		sedimentary	
		PC024B (m)			
Warra	43° 3' S	WR011B (y)	400 m	Jurassic	1998
	146° 42' E	WR004A (m)		dolerite	
		WR011E (m)			
Manuka	43° 6' S	WR008B (y)	200 m	Jurassic	1999
	146° 41' E	WR008A (m)		dolerite	
		WR008G (m)			
Kermandie	43° 13' S	KD022H (y)	300 m	Jurassic	1996
	146° 53' E	KD021C (m)		dolerite	
		KD022C (m)			

Since this study compares young forest regenerating following clearfelling and a regeneration burn with mature forest naturally regenerated following wildfire, logging and successional age effects are confounded. The species composition of vascular plants (Hickey 1994; Turner 2003), bryophytes (Turner 2003), and litter dwelling beetles (Baker *et al.* 2004) is similar in older logging regrowth compared to natural wildfire regeneration. Thus, while young logging regeneration may have some differences compared to natural regeneration of the same age, beetles collected in this study are expected to be reasonably representative of a ‘natural’ early successional community.

Sampling methods

Three replicate transects of pitfall traps were randomly positioned within each of the eight study areas (4 sites x 2 ages). At each site, the mature and young forest transects were separated by distances of approximately 300 – 1,500 m. Each transect was 99 m long, with pitfall traps located at the following distances from starting points: 1 m, 5 m, 10 m, 25 m, 50 m and 100 m (144 traps in 24 transects). The transects were located away from known environmental gradients (riparian zones and edges of clearfelled logging areas). This sampling design with unequal distances between traps within transects was developed as part of the broader sampling program investigating environmental gradients; concentrating sampling effort in the region where gradient effects are expected is a common approach, and spatial autocorrelation and pitfall-trap depletion effects were not measurable within the 99 m transects, based on the same dataset (Chapter 2).

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Pitfall traps consisted of 7.5 cm diameter plastic drinking cups inserted in PVC downpipe sleeves dug into the soil. Ethylene glycol (antifreeze) was used as preservative. A plastic lid was held in place above each trap with three wooden sticks

to protect traps from rainfall and disturbance by animals. Pitfall traps were closed for at least three weeks before trapping to avoid digging-in effects. Traps were operated for three separate one-month periods: winter (June – July 2001), spring (October – November 2001) and summer/autumn (February – March 2002). All beetles were removed and identified to species or morphospecies.

Statistical analysis

Data from the three pitfall trapping periods were pooled for analysis.

Age and site effects on the total abundance and number of species of beetles were investigated using ANOVA. The analyses used transect totals for the abundance and species richness of all beetles, providing three replicates. Tukey's Honestly Significant Difference (HSD) method investigated pair-wise comparisons. These tests were carried out in R Version 2.0.1 (R Development Core Team 2003).

Subsequent statistical analyses were conducted on a subset of the 37 most common beetle species, based on an arbitrary abundance cut-off of 0.05% of the total number collected.

Indicator species analysis (Dufrêne & Legendre 1997) in PC-ORD (McCune & Mefford 1999) assessed the habitat preferences of the commonly collected beetle species for mature and young forest. This analysis calculates an Indicator Value (IV, %) for each species, where 0 represents no indication and 100 represents perfect indication of that habitat. IV combines information about species' relative abundance (specificity) and relative frequency of occurrence (fidelity) in each of the forest successional ages (Dufrêne & Legendre 1997; McGeoch *et al.* 2002). An indicator value of 100% would denote that a species is only found in that habitat, and was collected in all samples from that habitat (Dufrêne & Legendre 1997). The analysis was based on the average abundances of beetle species in mature and young forest

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for each site, as this is the appropriate exchangeable unit for the permutation test (Anderson & Ter Braak 2003). A Monte Carlo *P*-value (9999 permutations) evaluates the statistical significance of the IV for each species. I follow Dufrêne and Legendre (1997) in assuming a species is characteristic of a habitat if the species IV is >25% and significant, but due to low statistical power in the permutation test with 4 replicates, $\alpha = 0.1$ was used to reduce the type II error rate.

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Permutational Multivariate Analysis of Variance (PERMANOVA V. 1.6, Anderson 2001, 2005) was used to test the beetle assemblage composition response to successional age and site differences. A factorial design was used in which fixed factors Site and Age were tested with 9999 permutations of residuals under the full model, using square-root transformed abundance data. The analysis used transect totals for the abundance of each common species, providing three replicates for each site/forest age combination. The permutation test *P*-value was referred to for the overall PERMANOVA model, since the number of unique values of the test statistic approached the number of permutations. For pair-wise *a posteriori* comparisons, the Monte Carlo asymptotic *P*-value was referred to since there were few unique values for the test statistic (Anderson 2005).

Non-metric multidimensional scaling (NMS) was used to illustrate patterns in beetle assemblage composition in relation to forest age and site differences. Square-root transformed data from each pitfall trap were used in this analysis. This was conducted in PC-ORD Version 4.10 (McCune & Mefford 1999) in 'slow and thorough' autopilot mode.

Results

Abundance and richness

Abundance and species richness were somewhat lower in mature than in young forest. Of 5,412 beetles collected, 42% were from mature forest traps. Abundance of beetles per transect was significantly lower in mature (188 ± 19 , mean \pm SE) than young (262 ± 22) forest (Table 2). Abundance also differed somewhat among sites. A Tukey's HSD test found beetle abundance was significantly greater at Kermandie compared to Manuka and Warra sites, but other pair-wise site comparisons were not significantly different. Of 349 morphospecies, 192 were recorded in mature forest and 259 in young forest. ANOVA of species richness found a significant interaction between forest age and sites (Table 2). A Tukey's HSD test indicated significantly greater species richness in young than mature forest at Picton. Species richness in young forest at Kermandie was also greater compared to both young and mature forest at Manuka, and compared to mature forest at Picton, although this probably relates more to site than age differences. Other Site x Age combinations did not differ significantly in species richness.

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Table 2 ANOVA on site and successional age effects on the total abundance and species richness of litter beetles.

Source	d.f.	Abundance			Species Richness		
		MS	F	P-value	MS	F	P-value
Site	3	15198	4.5494	0.01730	446.94	7.3926	0.002515
Age	1	33301	9.9688	0.00610	352.67	5.8332	0.028057
Site x Age	3	4318	1.2924	0.31108	219.67	3.6334	0.035837
Residual	16	3341			60.46		

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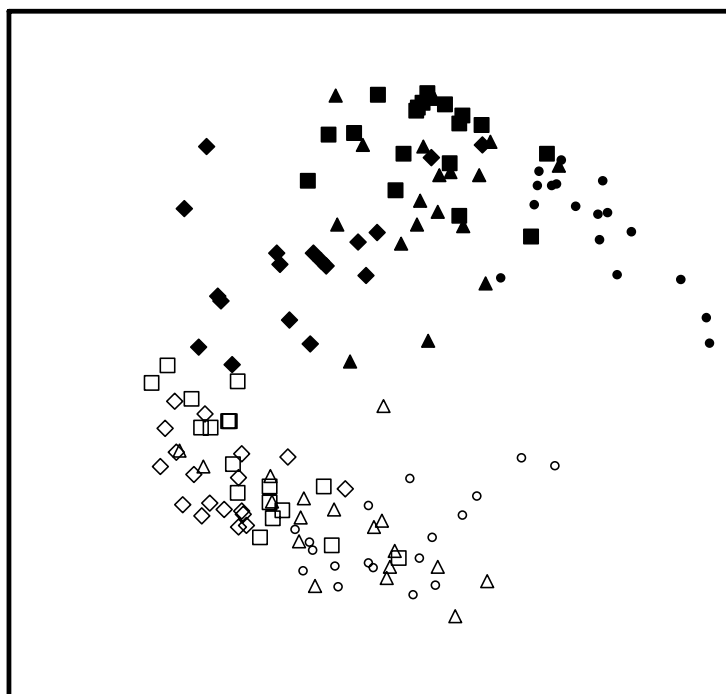
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Beetle community response to forest age and sites

Ordination of beetle assemblages in relation to forest age and site differences (Figure 1) illustrates that age is the stronger influence on beetle assemblages. There was no overlap amongst plots from the two forest ages, while overlap in assemblage composition was apparent amongst study sites within each forest age. None of the habitat structural variables measured from 1 m x 1 m quadrats (data not presented) were significantly correlated with the ordination space.

Fig. 1 Non-metric multidimensional scaling of beetle assemblages in two forest ages and four sites. The x-axis represents 24%, and the y-axis 49% of the variation in the dataset. The third dimension (not illustrated) explained 7% of variation. Stress = 16.5% and Instability = 0.00001 for a 3-dimensional solution after 400 iterations. Open symbols indicate mature forest, closed symbols young forest, diamonds are Kermadec, squares are Picton, triangles are Warra, and circles are Manuka.



Permutational multivariate ANOVA provides a statistical test of the community patterns illustrated in Figure 1. This test indicates that beetle assemblages were responding to both forest age and study sites, and these factors have a significant interaction (Table 3).

Table 3 Permutational multivariate ANOVA for litter beetle assemblages at four study sites and two successional ages.

Source	d.f.	MS	F	<i>P</i> -value
Site	3	3539.08	5.5034	0.0001
Age	1	26595.80	41.3572	0.0001
Site x Age	3	1680.39	2.6131	0.0002
Residual	16	643.08		

Significantly different beetle assemblages occurred in unlogged mature and young logging regeneration forest at all study sites (Table 4). While the *P*-value at Kermadie was closer to alpha than for the other three sites, the clear distinction of the young plots from the mature forest plots in the ordination suggests that this is unlikely to be a Type I error.

All pair-wise comparisons indicated significantly different beetle assemblages amongst sites within young forest; however only two pair-wise site comparisons (Manuka versus Kermadie and Picton) indicated significant differences in mature forest (Table 5). In Moran's (2003) arguments against the use of the sequential Bonferroni correction in ecological studies, he notes, "many significant results in a table indicate something important is happening", even when all *P*-values are relatively close to alpha. The two pair-wise site differences in mature

forest where $P < 0.05$ might possibly be spurious, but the young forest site differences in beetle composition are most likely to be real. In Figure 1, site differences were more apparent for young forest; although for mature forest, the Manuka plots were clustered separately in ordination space.

Table 4 Pair-wise *a posteriori* comparisons of successional age on beetle assemblages at each study site.

Site	t	P-value
Kermandie	2.3878	0.0187
Picton	4.1270	0.0031
Warra	3.5816	0.0036
Manuka	3.8184	0.0035

Table 5 Pair-wise *a posteriori* comparisons of study sites site on beetle assemblages among Kermandie (K), Picton (P), Warra (W) and Manuka (M) localities, conducted separately for each forest successional age.

Comparison	Mature		Young	
	t	P-value	t	P-value
K vs. P	1.6670	0.0757	2.6870	0.0105
K vs. W	1.8648	0.0526	2.2955	0.0164
K vs. M	1.9784	0.0351	2.8737	0.0090
P vs. W	1.1510	0.2946	1.9444	0.0387
P vs. M	1.8434	0.0491	2.0472	0.0396
W vs. M	1.4804	0.1385	2.0312	0.0342

Indicator species

Indicator species analysis identified seven species characteristic of mature forest and nine species characteristic of young forest (Table 6). Of the commonly collected species, seven species were not collected in mature forest but only one species was absent from young forest, *Decilaus striatus* (Curculionidae). The average Indicator Value of young regeneration forest characteristic species (99%) was also slightly higher than mature forest characteristic species (94%). Beetle species with a preference for young forest are possibly more stenotypic in their habitat use than those that prefer mature forest.

Of the 21 species that were not identified as being ‘characteristic’ of age class, many were nevertheless more than twice as abundant in either young or mature forest, suggesting those species may have an age-class preference. Of particular interest are *Cyphotrechodes gibbipenni* and *Homethes elegans* (both Carabidae) that were absent in mature forest, but were not considered characteristic of young forest since they were not collected at the Kermandie site. Anthicidae TFIC sp 02 also appeared to have a preference for young forest, although two specimens were collected in mature forest at Manuka, and none were collected in young forest at Kermandie. It is not clear whether the absence of these three species at Kermandie relates to the greater geographical separation or to the older regeneration at this site. *Eupines* CHANDLER 'Tasmania 1' (Staphylinidae) was only collected in young forest at the Picton site. *Baeocera* TFIC sp 02 (Staphylinidae) is the only species which could be classified as a *habitat generalist* with any confidence, with similar abundance and %IV in young and mature forest.

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Table 6 Abundance and Indicator Value (%) for common beetle species in mature unlogged forest and young logging regeneration. Species with an overall Indicator Value > 25% and permutation test *P*-value <0.1 are characteristic species of either forest age.

Species	Abundance		Indicator Value		<i>P</i> -value	
	Mature	Young	Mature	Young		Overall
<i>Species characteristic of mature forest</i>						
Leiodidae: Cholevinae: <i>Choleva</i> TFIC sp 01	79	8	91	7	90.8	0.0283
Leiodidae: Cholevinae: <i>Austronemadus</i> TFIC sp 03	201	7	97	1	96.6	0.0290
Staphylinidae: Aleocharinae: <i>Aleoc</i> _1	364	75	83	17	82.9	0.0564
Staphylinidae: Aleocharinae TFIC sp 02	32	1	97	1	97	0.0283
Melandryidae: Melandryinae: <i>Orchesia alphabetica</i> Lea	38	2	95	2	95	0.0283
Curculionidae: Cryptorhynchinae: <i>Decilaus nigronotatus</i> Lea, 1913	40	1	98	1	97.6	0.0283
Curculionidae: Cryptorhynchinae: <i>Decilaus striatus</i> Lea, 1913	85	0	100	0	100	0.0283
<i>Species characteristic of young forest</i>						
Carabidae: Carabinae: <i>Scopodes sigillatus</i> Germar, 1848	1	77	0	99	98.7	0.0283
Carabidae: Psydrinae: <i>Mecyclothorax ambiguus</i> (Erichson, 1842)	0	370	0	100	100	0.0283
Leiodidae: Leiodinae: <i>Zeadolopus</i> sp3	1	58	0	98	98.3	0.0570
Staphylinidae: Pselaphinae: <i>Anabaxis</i> CHANDLER 'Type 1'	2	545	0	100	99.6	0.0283
Staphylinidae: Pselaphinae: <i>Rybaxis parvidens</i> Lea, 1911	1	30	1	97	96.8	0.0283
Scirtidae: <i>Pseudomicrocara</i> TFIC sp 02	0	30	0	100	100	0.0283
Byrrhidae: Byrrhinae: <i>Microchaetes scoparius</i> Erichson, 1842	3	236	0	99	98.7	0.0283
Byrrhidae: Byrrhinae: <i>Pedilophorus mixtus</i> Lea, 1907	0	84	0	100	100	0.0283
Chrysomelidae: Galerucinae: <i>Arsipoda variegata</i> (Westwood, 1838)	0	34	0	100	100	0.0283

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Species	Abundance		Indicator Value			P-value
	Mature	Young	Mature	Young	Overall	
<i>Other species</i>						
Carabidae: Trechinae: <i>Cyphotrechodes gibbipennis</i> (Blackburn, 1901)	0	56	0	75	75	0.1419
Carabidae: Trechinae: <i>Sloaneana tasmaniae</i> (Sloane, 1915)	67	137	33	50	50.4	0.8279
Carabidae: Broscinae: <i>Promecoderus longus</i> Sloane, 1920	31	9	78	11	77.5	0.1421
Carabidae: Pterostichinae: <i>Notonomus politulus</i> (Chaudoir) 1865	46	24	49	17	49.3	0.4876
Carabidae: Pterostichinae: <i>Rhabdotus reflexus</i> (Chaudoir, 1865)	141	59	71	22	70.5	0.2572
Carabidae: Agoninae: <i>Homethes elegans</i> Newman, 1842	0	42	0	75	75	0.1419
Leiodidae: Cholevinae: <i>Nargomorphus?</i> sp 1	94	34	73	13	73.4	0.1135
Leiodidae: Cholevinae: <i>Nargomorphus?</i> sp 2	30	17	48	9	47.9	0.3708
Leiodidae: <u>Coloninae: <i>Colon</i> sp. 1</u>	3	55	1	95	94.8	0.1141
Staphylinidae: Microsilphinae: <i>Microsilpha</i> 'ANIC Thayer sp 15'	41	12	19	6	19.3	1
Staphylinidae: Pselaphinae: <i>Eupines</i> CHANDLER 'Tasmania 1'	0	91	0	50	50	0.4269
Staphylinidae: Pselaphinae: <i>Sagola?</i> sp	28	1	48	1	48.3	0.4264
Staphylinidae: Aleocharinae: <i>Aleoc</i> 44	79	14	64	11	63.7	0.3141
Staphylinidae: Scaphidiinae: <i>Baeocera</i> TFIC sp 02	20	21	37	38	38.4	1
Staphylinidae: Oxytelinae: <i>Anotylus</i> TFIC sp 04	4	34	3	45	44.7	0.7141
Staphylinidae: Staphylininae: <i>Quedius</i> 'ANIC Newton sp 03'	9	37	20	80	80.4	0.4279
Staphylinidae: Staphylininae: Staphylininae TFIC sp 03?	40	87	24	34	34.3	0.829
Nitidulidae: Nitidulinae: <i>Thalycrodes australe</i> (Germar, 1848)	9	21	15	70	70	0.2561
Nitidulidae: Nitidulinae: <i>Thalycrodes cylindricum</i> Blackburn, 1891	51	3	71	4	70.8	0.3169
Anthicidae: Anthicidae TFIC sp 02	2	37	1	71	71.2	0.1419
Curculionidae: Cryptorhynchinae: <i>Roptoperus tasmaniensis</i> Lea, 1913	65	45	59	31	59.1	0.4839

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Discussion

Young logging regeneration and mature unlogged *Eucalyptus obliqua* dominated forests were found to support very different litter-dwelling beetle assemblages. While it may be reasonable to assume that these differences are largely attributable to successional age rather than logging history differences (see Baker *et al.* (2004)), it would be preferable to test this assumption. Future wildfires may allow natural benchmarks for early regeneration in such studies, but at the current time no such sites were available.

Forest age effects had a much stronger influence on beetles than did site effects. Beetle abundance was higher in young forest than in mature forest, and species richness was similar or greater, illustrating that beetles quickly colonize following harvesting and burning. Pitfall traps measure activity density rather than actual population density, and the catch of certain species may have been influenced by different habitat structures in mature and regeneration forest (Greenslade 1964; Melbourne 1999); although habitat structural variables were not significantly correlated with patterns of beetle occurrence. Nevertheless, striking differences in assemblage composition are apparent, demonstrating that species composition shifts with forest age.

Beetle assemblage composition was distinctly different in young compared to mature forest in this study, with nearly half the common beetle species identified as being characteristic of successional age. One habitat generalist species, *Baeocera* TFIC sp 02 (Staphylinidae), was equally abundant in both mature and young forest, while all other species were considerably more abundant in a particular successional age for which they possibly had a preference, even if they were not specific to that age.

More overlap would be expected with the addition of intermediate age classes, as was found in the chronosequence studies of Michaels (Michaels & McQuillan 1995; Michaels & Bornemissza 1999; Michaels 1999). Young forest may support species that have colonised the recently harvested and burned habitat, along with mature forest species initially surviving the disturbance, which may disappear in intermediate successional stages (Niemelä *et al.* 1993; Michaels & McQuillan 1995). This may be an explanation for greater abundance and species richness in young forest (Butterfield & Coulson 1983; Niemelä *et al.* 1993; Michaels & McQuillan 1995). Another explanation may be that elevated nutrient availability in the surface soil following the regeneration burn (Ellis & Graley 1983; Khanna & Raison 1986; Tomkins *et al.* 1991) could increase the availability of soil-dwelling prey, and thus predatory beetle abundance. This study recorded a higher proportion of beetles from predatory taxa amongst the species characteristic of young compared to mature forest (Lawrence & Britton 1994).

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Site differences in beetle assemblage composition were greatest among young forest sites, but were also apparent in mature forest. The differences represented in the range of habitat conditions from the low seedling cover in one-year-old forest through to tall, dense cover of trees in five-year-old forest appear to have a greater influence on beetles than the age differences probably represented within mature forest sites, although as noted in the Methods section we were unable to determine exact site ages of mature forest in this study. The prevalence in the landscape of mixed-age mosaics as well as single-aged stands (Hickey *et al.* 1998; Alcorn *et al.* 2001) possibly means that Tasmanian mature forest litter beetles are adapted to a wider range of conditions. This is supported by a study by Driscoll (2005) that found relatively little difference in the beetle assemblages in Tasmanian mature eucalypt forest and rainforest (a later successional stage, Jackson 1968).

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Additional reductions in old-growth habitat, fragmentation and altered spatial distribution and stand-areas distinguish timber harvesting areas from forest subject only to the natural wildfire regime (Baker *et al.* 2004). This may impact beetle population dynamics across the landscape, especially since beetle species distributions are patchily distributed. The degree of habitat specificity and matrix permeability will affect how readily beetles will disperse amongst patches of preferred habitat, thus affecting metapopulation dynamics and extinction risk (Ås 1993; Davies *et al.* 2004; Driscoll 2005). Since nearly half the beetle species occurring commonly in wet *E. obliqua* forest were found to be specialists for forest age, these concepts may have relevance in Tasmania's managed forest landscape. For generalists, and species that readily disperse through the matrix, metapopulation and island biogeography dynamics are probably less relevant (Driscoll 2005). Davies *et al.* (2004) found that rare, habitat specialist beetles were especially sensitive to fragmentation. More research is warranted into the consequences of fragmentation and changes to the age-structure of forest caused by current harvesting practices.

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There was some agreement about the habitat preferences of individual beetle species with other Tasmanian studies. Michaels (Michaels & McQuillan 1995; Michaels 1999) also identified *Mecyclothorax ambiguus* and *Scopodes sigillatus* as preferring early regeneration. *Homethes elegans*, which was absent from mature forest in this study, but was not classified as characteristic of young forest due to its absence at one study site, was designated a young forest indicator species by Michaels (1999). Four species of *Lissotes* (Lucanidae) were collected in this study, but uncommonly, so no comparisons are made with Michaels and Bornemissza (1999). All species classified as mature forest specialists in the current study were also collected occasionally (<25 individuals) in 33-year-old regeneration forest (Baker 2000), while *Aleoc_1* (Aleocharinae) was common in 33-year-old forest

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(Baker *et al.* 2004). Of the species characteristic of young regeneration forest, *Rybaxis parvidens* (Staphylinidae) was occasionally collected in intermediate-aged regeneration (Baker 2000). While this emphasises the value of studying intermediate successional ages, indicator species specifically for mature and young forest are potentially the most useful for quantifying logging impacts. For example, one could assess the response of mature forest indicators to edge effects or to habitat islands in Variable Retention silvicultural systems (Bashford *et al.* 2001; Hickey *et al.* 2001).

Invertebrate biodiversity studies are labour intensive, and often subsets of taxa are used for bioindication purposes. Carabid beetles are possibly the most widely used invertebrate indicator taxa (e.g. Refseth 1980; Rykken *et al.* 1997, Niemelä, 1993 #367; Rainio & Niemelä 2003). In this study, only two of the sixteen significant indicator species were carabids, and these were both indicators of young forest. Eight beetle families were represented, of which the Staphylinidae (four species) had the greatest number of indicator species. While carabids have been shown to be sensitive indicators (Rainio & Niemelä 2003), it would seem preferable, when possible, to use all litter-dwelling Coleopterans rather than only carabids for bioindication. The diversity of feeding niches and trophic levels, dispersal ability and habitat preferences amongst all of the Coleopteran families is much greater than amongst the carabids alone (Lawrence & Britton 1994).

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In summary, this study enhances our understanding of litter-dwelling beetle ecology in Tasmania, by demonstrating that beetles have successional age preferences that outweigh species turnover amongst sites in a spatially replicated study design. Indicator species for young and mature wet eucalypt forest are available for reference in other silvicultural studies. The findings here suggest that carabids alone might not provide effective indicators of habitat preferences in wet eucalypt forest, and use of a wider range of beetle taxa would be preferred.

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Chapter 6

Estimating edge effects on ground-dwelling beetles at clearfelled non-riparian stand edges in Tasmanian wet eucalypt forest

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Preface: This chapter documents the depth of edge penetration from logging coupes into non-riparian forest. Reference is made to indicator species of forest age (Chapter 5). Edge-avoiding mature forest species are also identified, and are referred to in following chapters.

Abstract

Edge effects potentially have negative consequences for biodiversity in logging areas. In Tasmanian wet eucalypt forest, ground-dwelling beetle assemblages responded to habitat edges between mature unlogged forest and young regeneration following clearfelling. Transects of pitfall traps extended 100 m into unlogged forest and 10 m into the felled area firebreaks at four study sites (4 sites x 3 transects x 8 traps/transect = 96 traps). The depth of edge influence extended between 10 m and 25 m into mature forest, and the beetle assemblage was estimated to be 95% similar to interior forest at approximately 22 m from the edge. The species composition of beetles changed gradually with distance from the edge, but for practical purposes we distinguished three zones of edge response: mature forest interior extending ≥ 22 m into unlogged forest, firebreak habitat at the edge of the coupe that extends 1 m into unlogged forest, and an edge-affected mature forest zone in between. Individual species known to be characteristic of mature and young forest were of greatest indicator value in mature forest interior and firebreak habitat respectively. *Choleva* TFIC sp 01 (Leiodidae), *Decilaus nigronotatus*, *D. lateralis* and *D. striatus* (all Curculionidae) were identified as indicator species characteristic of mature forest interior. No species were found to be characteristic of the habitat edges.

These results are relevant to current management practices in Tasmanian wet eucalypt forest, in particular to the efficacy of linear reserve networks. One hundred metre wide wildlife habitat strips, when bounded by recently harvested forest, are estimated to contain a little over 50% of interior habitat not compromised by edge effects. Small patches of forest (< 1 ha) retained in variable retention harvesting are predicted to contain little or no uncompromised interior habitat for ground-dwelling beetles.

Introduction

Clearfell logging creates abrupt edges between harvested stands (coupes) and adjacent unlogged mature forest. Thus, in managed forest landscapes composed of relatively small (10-100 ha) coupes of different age, harvesting may increase the extent, and severity, of edges between different habitats compared to natural wildfire-regenerated landscapes (Peltonen et al., 1997; Baker et al., 2004). Edge effects occur where two structurally dissimilar landscape components abut each other, leading to ecological changes near the boundary of the adjacent habitats (Peltonen et al., 1997). Both abiotic and biotic gradients are recorded at forest edges; e.g. microclimate, distribution and abundance of species, species interactions, vegetation structure (Matlack, 1993; Fraver, 1994; Kapos et al., 1997; Peltonen et al., 1997). Edge effects at wet forest logging coupes in Tasmania, Australia have previously been documented for vegetation, microclimate and the frog *Crinia signifera* (Westphalen, 2003; Tabor et al., submitted; Appendix 5), but not for invertebrates.

Documenting the ecology of habitat edges is an important field of landscape conservation biology since certain habitat specialist species avoid edges, and thus may be negatively impacted by habitat fragmentation and edge effects (Yahner, 1988; Murcia, 1995; Ries et al., 2004; Lindenmayer and Burgman, 2005). An understanding of how edge effects influence the ground-dwelling Coleoptera will help in assessing the likely landscape-level fragmentation impacts of different silvicultural options (e.g. coupe sizes and harvesting systems) and also the ecological benefits of uncut reserves such as wildlife habitat strips. Narrow linear reserves are known to suffer edge effects (Soulé and Gilpin, 1991; Niemelä, 2001) and thus their integrity and usefulness for conservation warrants examination. Ratios of edge to

interior forest will affect the core area available for edge-avoiding species (Laurance and Yensen, 1991; Sisk and Margules, 1993). For example, predictions based on an edge study of birds suggested that blocks of habitat > 100 ha are required to effectively buffer interior habitat (Sisk and Margules, 1993).

The penetration depth of edge influence (DEI) (Ries et al., 2004) varies greatly amongst different abiotic and biotic factors, with differing sensitivities even among closely related species (Laurance et al., 1997; Peltonen et al., 1997; Ries et al., 2004). For a particular factor, DEI can also vary with local edge conditions such as aspect (Yahner, 1988; Turton and Freiburger, 1997; Ries et al., 2004). DEI may be greater for invertebrates than for vegetation and microclimate (Didham, 1997; Laurance et al., 1997). Most previous studies have found the effects of edges on invertebrates disappear within the first 100 m into the forest (Murcia, 1995; Didham, 1997; Davies et al., 2001; Ries et al., 2004), although some edge effects may extend for kilometers (Laurance, 2000).

We examined the edge response of ground-dwelling beetles to recently clearfelled logging coupe edges in Tasmania. Forest ground-dwelling beetles have been demonstrated to be sensitive to edge effects elsewhere (Helle and Muona, 1985; Spence et al., 1996; Didham, 1997; Magura and Tóthmérész, 1997; Davies and Margules, 1998; Heliölä et al., 2001), and in damp sclerophyll forest in northeast Tasmania (Grove and Yaxley, 2005). Ground-dwelling beetles are responsive to habitat conditions and forest structure, including factors such as vegetation composition, microclimate, solar radiation, the number and condition of rotting logs, and structural and chemical attributes of the soil and leaf litter (Greenslade, 1968; Niemelä and Spence, 1994; Humphrey et al., 1999; Yee, 2005). However, the specific habitat requirements for most forest ground-dwelling beetles in Tasmania are still unknown. Distinct communities of wet forest ground-dwelling beetles have

been documented in different stand ages (Michaels and McQuillan, 1995; Chapter 5). Edge effects, as well as other consequences of fragmentation (see also Driscoll, 2005), are therefore likely in Tasmania's managed forests. The responses of litter beetles to edge effects elsewhere are variable and species specific (Duelli et al., 1990; Didham et al., 1998a; Heliölä et al., 2001), so that edge-affiliated, edge-avoiding and neutral responses may be expected within the overall community.

Other environmental gradients could potentially impact DEI for certain species. In this paper we investigate non-riparian coupe edges where edge effects are not confounded with riparian influences, which have been demonstrated to cause changes to the abundance, species richness and assemblage composition of ground-dwelling beetles in Tasmanian wet eucalypt forest (Chapter 3; Chapter 4). Our study addresses the following objectives.

Objectives

1. To estimate the depth of edge influence for ground-dwelling beetle assemblages at non-riparian edges where mature unlogged forest abuts recently clearfelled forest.
2. To identify indicator species that characterise the interior forest.
3. To test hypotheses that
 - a. Mature forest characteristic beetle species will be less common or absent in the edge transition zone and firebreak.
 - b. Young forest characteristic species will be more common in the coupe firebreak, and less common or absent in the mature forest interior.
4. To relate the depth of edge influence to current forest management practices and reserve prescriptions.

Methods

Study Sites and collection of beetles

This study was conducted in wet eucalypt forest with an overstorey dominated by *Eucalyptus obliqua*, with occasional *E. regnans* and *E. delegatensis*, and with a mixed sclerophyllous and rainforest understorey (Neyland, 2001). Since the 1960s, the standard harvesting and regeneration technique in tall, wet eucalypt forest has been to clearfell, burn and broadcast sow with eucalypt seed, nominally on a rotation of 80 - 100 years (Forestry Tasmania, 1998). However, in the future some aggregated retention harvesting, where 0.5-1 ha clumps are retained within coupes (Hickey et al., 2001), will also be used. After clearfelling, firebreaks approximately 10-15 m wide are mechanically cleared along the inner edge of coupe boundaries to protect adjacent unlogged forest from the high intensity regeneration burn (Westphalen, 2003). Removal of topsoil, and successful establishment of disturbance-adapted plants such as the tall sedge *Gahnia grandis* distinguish the firebreak from the coupe interior, even as the stands age. The study area, approximately 60 km WSW of Hobart in southern Tasmania, Australia, has soils largely derived from Jurassic dolerite and some from Permian sedimentary deposits.

Edge effects on ground-dwelling beetles were investigated at non-riparian coupe edges of four recently clearfelled and regenerated coupes (Table 1). The Warra and Manuka sites were located within the Warra Long Term Ecological Research site (Brown et al., 2001). Distance between sites ranged from 3 to 21 km. Coupes ranging from one to five years since the clearfelling regeneration burn (Table 1) were included to represent “early-age” edge effects.

Table 1. Characteristics of the study sites and coupe edges. ‘FT’ refers to Forestry Tasmania, ‘y’ indicates young forest and ‘m’ indicates mature forest areas.

	Study site			
	Picton	Warra	Manuka	Kermandie
Location	43°7’S	43°3’S	43°6’S	43°13’S
	146°42’E	146°42’E	146°41’E	146°53’E
FT Coupe	PC024A (y)	WR011B (y)	WR008B (y)	KD022H (y)
numbers	PC024B (m)	WR011E (m)	WR008K (m)	KD022C (m)
Clearfelled coupe regenerated	2000	1998	1999	1996
Elevation	160 m	350 m	150 m	340 m
Coupe edge studied	W	E	W	W
Mature forest slope relative to edge	upslope - steep	flat	downslope - gentle	downslope - steep
Influence of regeneration burn on mature forest	up to 25 m	up to 100 m	none	none

Edge effects are known to vary with edge age (Ranney et al., 1981; Matlack, 1994), thus it is possible that differences in edge penetration may occur within this age range, since vegetation in the firebreak varied in structure from the youngest coupe (Manuka), where only patchy low vegetation was growing on the firebreak, to the oldest coupe (Kermandie) where the firebreak was thick with ~2 m high *Gahnia*

grandis. One coupe edge adjacent to non-riparian mature forest was selected for study at each site. Because of their availability, suitable study sites were constrained to the four used, and it was not always possible to find edges that were not affected by escaped regeneration burns (see Table 1). Since regeneration burns commonly penetrate into unlogged forest (S. Baker, personal observation), we consider their impacts to be a part of the edge dynamics (analogous to the impacts of additional logging slash on edges, Westphalen, 2003).

Three transects were positioned perpendicular to the edge at each study site, at positions randomly located along the edge lengths. For each transect, the exact position of the edge was defined as a line connecting the outer bases of the two nearest uncut trees. Within each transect single pitfall traps were positioned at distances 1 m, 5 m, 10 m, 25 m, 50 m and 100 m into unlogged mature forest, and 5 m and 10 m into the coupe's firebreak (hereafter designated -5 m and -10 m). Eight traps, each in three transects within four study locations, resulted in a total of 96 pitfall traps. As with most forest attributes, edge effects can be measured at various spatial scales. A decision about the spatial scale at which edge effects were assessed in this study was made with regard to the likely magnitude of edge penetration based on other studies (≤ 100 m), and to designing a sampling program that did not confound edge gradients with elevation change, riparian influences, or vegetation boundaries.

Collecting samples at unequal distances along transects is a design commonly employed in studies of edge effects (e.g. Bedford and Usher, 1994; Didham et al., 1998a; Kotze and Samways, 2001; Dangerfield et al., 2003) since it concentrates sampling effort in the region where edge effects are considered most likely. However, this design risks confounding patterns in species composition and abundance with patterns attributable to spatial autocorrelation or pitfall trap

depletion. In order to rule out these confounding influences, data from equivalent transect designs in mature forest away from known environmental gradients were screened. Depletion and autocorrelation were demonstrated not to be a significant influence on pitfall catches of beetles in this forest type (Chapter 2). Edge effects can obviously extend on either side of logging coupe edges, and some studies have transects of equal length either side of an edge (Helle and Muona, 1985; Spence et al., 1996; Kotze and Samways, 2001). The focus of our study was on the mature forest beetle assemblages that may be negatively impacted by logging practices. Hence, transects extended 100 m into unlogged forest but only 10 m into the logged coupe firebreaks. Sampling the firebreak was intended to assist in quantifying edge penetration. However, firebreaks are more intensively disturbed than the rest of the coupe, and may have different beetle species composition. Beetle species composition in interior coupe and mature forest are described in Chapter 5.

Pitfall traps consisted of 7.5 cm diameter plastic drinking cups inserted in PVC downpipe sleeves dug into the soil. Ethylene glycol (antifreeze) was used as preservative. A plastic lid was held in place above each trap with three wooden sticks to protect traps from rainfall and disturbance by vertebrates. Pitfall traps were closed for at least three weeks before trapping to avoid digging-in effects. Traps were operated for three separate one-month periods: winter (June – July 2001), spring (October – November 2001) and summer/autumn (February – March 2002). All beetles were removed and sorted to family and morphospecies based on external morphology, using the protocols of Oliver and Beattie (1996) and keys to family in Lawrence and Britton (1994) and Lawrence *et al.* (1999). Identification to morphospecies enables acquisition of ecological knowledge in spite of the vast number of species and relatively poor taxonomic knowledge of Tasmanian ground-dwelling beetles. Many species await formal description, and identification keys are

generally unavailable, thus identification to taxonomic species was not possible for all morphospecies. Species identifications were made by reference to the Tasmanian Forest Insect Collection (TFIC) at Forestry Tasmania, where the reference collection will be deposited on completion of ongoing studies. This collection uses TFIC code numbers for beetle morphospecies that have not yet been identified.

Analyses

Data from the three pitfall trapping periods were pooled for analyses, after data screening confirmed that edge effects did not vary seasonally (Table 2), using a two-way crossed NPMANOVA model (Anderson, 2001; Anderson, 2003b) for Distance x Season within each study site. Omitting rare species (abundance < 0.5% that of the total) reduced the dataset from 2,868 beetles to 2,185 beetles in 41 morphospecies.

Nonlinear canonical analysis of principal coordinates (NCAP) was used to fit a logistic gradient to multi-species data to predict the depth of edge influence (Millar *et al.*, 2005). Specifically, we were interested in predicting the distance into mature forest at which the beetle community structure was 95% similar to interior forest. According to Millar *et al.* (2005), a logistic gradient may be appropriate for habitat boundaries, where it is reasonable to assume that the community structure changes most rapidly near the edge and the effect of the boundary diminishes with increasing distance. NCAP was conducted in R Version 2.0.1 (R Development Core Team, 2003) with code available from <http://www.stat.auckland.ac.nz/%7Emillar/NCAP/NCAP.html>. NCAP used Bray-Curtis dissimilarities of square-root transformed beetle abundance data, 6 principal coordinates and 9999 randomizations.

NPMANOVA was used to test the response of beetle assemblages to distance from edge and study sites using a two-way crossed model. 'Distance' (-10 m, -5 m, 1

m, 5 m, 10 m, 25 m, 50 m and 100 m from edge) and 'Site' (Picton, Warra, Manuka and Kermandie) were fixed factors (Downes et al., 2002). NPMANOVA analysis was conducted on square-root transformed abundance data using Bray-Curtis dissimilarities and 9999 unrestricted random permutations of the raw data, where the three transects at each site were considered replicates. The variance explained by each source in the NPMANOVA model was estimated using mean squares and sample sizes (Anderson, 2001; Quinn and Keough, 2002). Pairwise post-hoc comparisons of all distance combinations facilitated estimation of DEI. Following Moran (2003), we chose to apply logic to our interpretation of multiple comparisons, since sequential Bonferroni adjustment would risk greatly inflating the Type II error rate relative to the possible increase in the Type I error rate without adjustment.

CAP (canonical analysis of principal coordinates) is a constrained ordination approach that displays multivariate data by reference to specific hypotheses, finding dimensions that are best at discriminating among *a priori* groups (Anderson, 2003a; Anderson and Willis, 2003). CAP was conducted to illustrate patterns in beetles with respect to distance from coupe edge, based on pooled data from the three replicate traps at each distance from edge within sites. Data were square-root transformed and the Bray-Curtis distance measure was used. Correlation of species with canonical axes in CAP analysis can be used to identify species responsible for multivariate patterns (Anderson and Willis, 2003).

Indicator species analysis (Dufrêne and Legendre, 1997) in PC-ORD (McCune and Mefford, 1999) assessed the habitat preferences of beetle species for edge zones as defined by the previous analyses: Interior (25 m, 50 m and 100 m traps), Edge (5 m and 10 m traps) and Firebreak (-10 m, -5 m and 1 m). Indicator Species Analysis calculates an Indicator Value (IV, %) for each species, where 0 represents no indication and 100 represents perfect indication of that habitat. IV

combines information about species' relative abundance (specificity) and relative frequency of occurrence (fidelity) in each of the edge transition zones (Dufrêne and Legendre, 1997; McGeoch et al., 2002). An indicator value of 100% would denote that a species is only found in that habitat, and was collected in all samples from that habitat (Dufrêne and Legendre, 1997). The analysis was based on the average abundances of beetle species in the three edge zones for each site. A Monte Carlo *P*-value (9999 permutations) evaluated the statistical significance of the IV for each species by randomly reassigning abundances from each site to edge response zones. 'Site' is the appropriate exchangeable unit for the permutation test (Anderson and Ter Braak, 2003). We follow Dufrêne and Legendre (1997) in assuming a species is characteristic of a habitat if the species IV is >25% and significant, but due to low statistical power in the permutation test with 4 replicates, $\alpha = 0.1$ was used to reduce the Type II error rate.

Results

Although the beetle assemblage composition varied between the three seasonal trapping periods, there was no significant interaction between trapping season and distance from the coupe edge at any of the four study sites (Table 2). This suggests that beetles did not shift seasonally with respect to distance along the edge-interior gradient. Data from the three trapping seasons were therefore pooled to facilitate community analyses.

Fitting the logistic canonical correlation gradient with NCAP (Fig. 1) resulted in a correlation of 0.378 and was highly statistically significant (pseudo- $F = 0.2211$, $P = 0.0001$). The model predicts beetle assemblages are 95% similar to interior forest at 22.3 m from the coupe edge. Additionally, beetles were predicted to be 79% along

the gradient towards an interior assemblage by 10 m, 96% similar by 25 m, and 99% similar by 35 m from edges. Thus edge effects have effectively ceased by approximately 22 m into unlogged forest. While this result concurs with predictions of edge effects from NPMANOVA and CAP constrained ordination analyses (below), it should be interpreted as a prediction only, since noise in the dataset provided only medium strength of correlation, and confidence intervals extended over much of the gradient (e.g. at 22.3 m, 95% confidence intervals estimate that beetle assemblages are somewhere between 2% and 100% along the transitional gradient to interior forest). The redundancy statistic approach provided similar results to the canonical correlation approach reported here; the beetle assemblage was predicted to be 95% similar to interior forest by 23.2 m from the edge.

Fig. 1. NCAP plot of the logistic gradient (solid line) fitted to beetle assemblage data at eight distances from non-riparian forest edges.

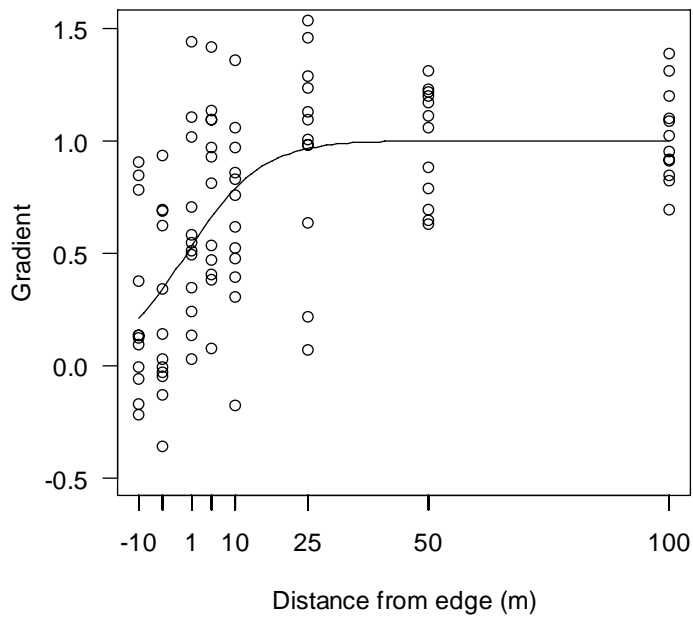


Table 2. NPMANOVA for litter beetle assemblages at the four study sites over three seasons and eight distances from coupe edges.

Source	Study Site							
	Picton		Warra		Manuka		Kermandie	
	MS	F	MS	F	MS	F	MS	F
Distance	7377.40	2.2265***	4618.45	1.2455^	6717.50	1.6966***	4210.05	1.1525 [#]
Season	21944.95	6.6229***	18736.18	5.0600***	14640.21	3.6976***	18205.88	4.9838***
Distance x Season	3095.28	0.9341 [#]	2885.52	0.7782 [#]	2553.59	0.6449 [#]	2524.00	0.6909 [#]
Residual	3313.49		3708.11		3959.42		3653.02	

Significance levels [#]p ≥ 0.1; ^p < 0.1; *p < 0.05; **p < 0.01; ***p < 0.001

d.f.: Distance = 7, Season = 2, Season x Distance = 14, Residual = 48

NPMANOVA analysis found that beetle assemblages differed significantly between study sites and distances from coupe edges (Table 3). Variance components analysis indicated that differences in beetle assemblages amongst study sites are stronger than differences due to edge effects (Table 3). Pairwise comparisons amongst the distances (Fig. 2) illustrate the transitional nature of the edge response, with overlapping zones of edge response from the firebreak, to edge-affected mature forest, to mature forest interior. These results suggest that the depth of edge influence extends from between 10 m and 25 m into unlogged mature forest.

Table 3. Non-parametric multivariate analysis of variance (NPMANOVA) using Bray-Curtis dissimilarities for litter beetle assemblages at four sites and eight distances from coupe edges.

Source	d.f.	SS	MS	F	P	Variance %
Site	3	58875.96	19625.32	7.4618	0.0001	19.8
Distance	7	36943.42	5277.631	2.0066	0.0001	6.1
Site x Distance	21	57621.19	2743.866	1.0432	0.3191	1.1
Residual	64	168327.4	2630.116			73.1
Total	95	321768				

Fig 2. Pairwise comparisons from NPMANOVA analysis. Beetle assemblages from edge distances joined by solid lines do not differ significantly ($P > 0.05$) from each other. A non-significant pairwise comparison between 1 m and 50 m plots is not illustrated.

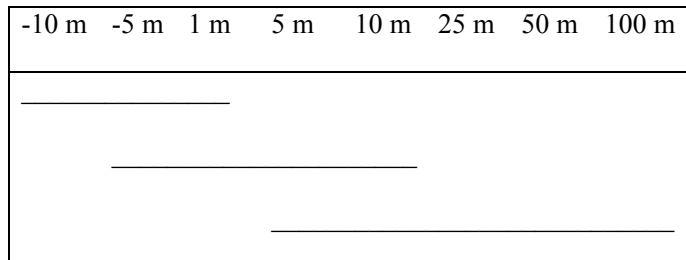
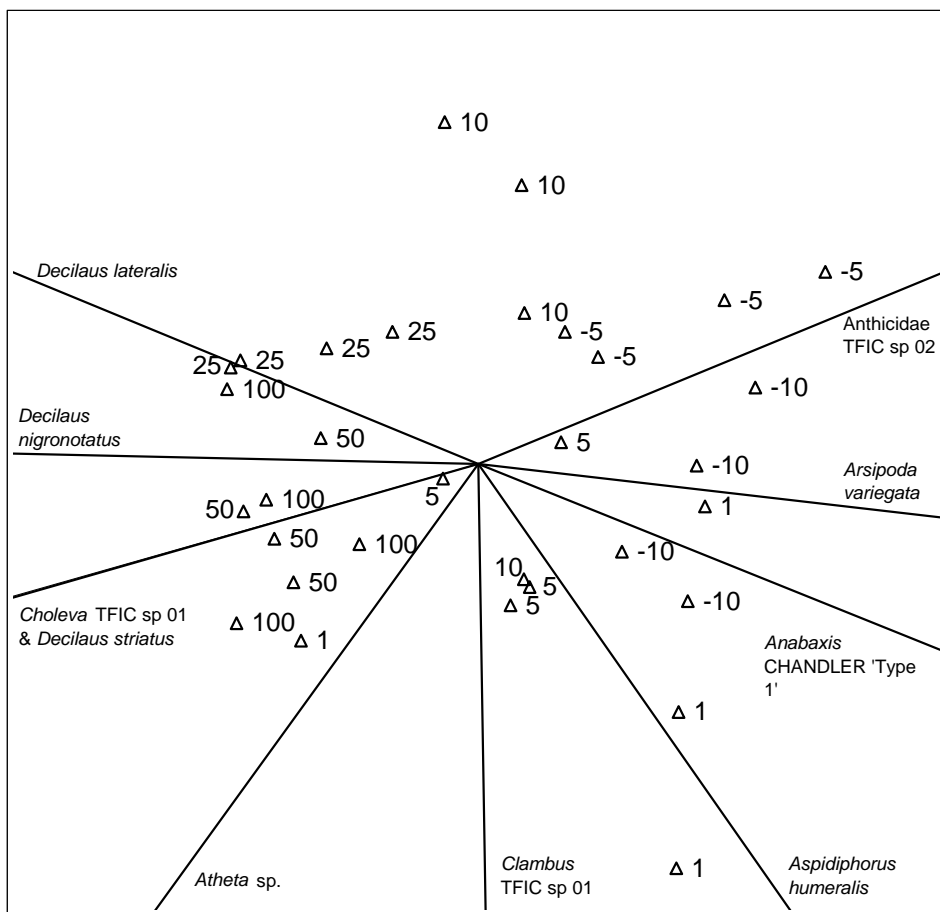


Fig 3. Constrained CAP ordination of beetle assemblages in relation to distance from logging coupe edge (illustrated, in metres) at four study sites. Vectors are plotted for species that are correlated with the ordination with $r > |0.5|$.



The CAP ordination (Fig. 3) maximises separation amongst distances from coupe edges rather than the more influential site differences (not illustrated). This ordination also illustrates the transitional response of beetle assemblages at forest edges. In particular, there is separation of the distances from edge along the horizontal-axis, with interior forest plots (25–100 m into uncut forest) positioned to the left, edge-affected mature forest plots (5 m and 10 m) in the middle, and firebreak plots (1 m, -5 m and -10 m) positioned towards the right. Beetle assemblages 1 m into uncut forest are more similar to those in the coupe firebreak than to edge-affected mature forest further from the edge. Based on the separation of distance categories along the horizontal-axis of Fig. 3, as well as results from NCAP and NPMANOVA analyses, the previous three edge response zones were designated to facilitate Indicator Species Analysis.

Several of the beetle species that were correlated with the ordination space were indicator species characteristic of mature or young forest (Chapter 5). *Atheta* sp. (Staphylinidae: Aleocharinae), *Decilaus striatus* Lea, 1913 and *D. nigronotatus* Lea, 1913 (both Curculionidae) and *Choleva* TFIC sp 01 (Leiodidae) are characteristic of mature forest while *Arsipoda variegata* (Westwood, 1838) (Chrysomelidae) and *Anabaxis* CHANDLER 'Type 1' (Staphylinidae: Pselaphinae) are characteristic of young forest. Anthicidae TFIC sp 02 was also considered to prefer young forest (Chapter 5), although it was not classified as 'characteristic' of this habitat. That mature forest indicator species were correlated in the direction of interior forest points, and young forest indicators were correlated in the direction of firebreak points, provides additional support to suggest that separation of points along the horizontal-axis is in response to edge effects.

Table 4. Indicator Value (%) for beetle species in the coupe firebreak (-10 m, -5m and 1 m), mature forest edge habitat (5 m and 10 m) and mature forest interior habitat (25 m, 50 m and 100 m from edge). Species with permutation test *P*-value <0.1 are indicators of forest edge conditions (shown in bold type).

Species	Indicator Value				P-value
	Firebreak	Edge	Interior	Overall	
<i>Species characteristic of mature forest</i>					
Leiodidae: Cholevinae: <i>Choleva</i> TFIC sp 01	1	6	82	81.7	0.0180
Leiodidae: Cholevinae: <i>Austronemadus</i> TFIC sp 03	2	31	49	49.2	0.3925
Staphylinidae: Aleocharinae: <i>Atheta</i> sp. (Aleoc_1)	35	30	36	35.7	0.9253
Melandryidae: Melandryinae: <i>Orchesia alphabetica</i> Lea	3	31	45	45.5	0.4539
Curculionidae: Cryptorhynchinae: <i>Decilaus nigronotatus</i> Lea, 1913	2	12	68	68.0	0.0365
Curculionidae: Cryptorhynchinae: <i>Decilaus striatus</i> Lea, 1913	7	7	71	71.4	0.0561
Curculionidae: Cryptorhynchinae: <i>Decilaus lateralis</i> Lea, 1913¹	0	17	67	66.7	0.0547
Avarage IV's	7.1	17.1	57.0	56.9	
<i>Species characteristic of young forest</i>					
Carabidae: Carabinae: <i>Scopodes sigillatus</i> Germar, 1848	34	19	20	34.4	0.8526
Carabidae: Psydrinae: <i>Mecyclothorax ambiguus</i> (Erichson, 1842)	69	2	0	69.3	0.1033
Staphylinidae: Pselaphinae: <i>Anabaxis</i> CHANDLER 'Type 1'	77	13	3	77.4	0.0388
Staphylinidae: Pselaphinae: <i>Rybaxis parvidens</i> Lea, 1911	50	0	0	50.0	0.2738
Byrrhidae: Byrrhinae: <i>Microchaetes scoparius</i> Erichson, 1842	51	36	10	51.3	0.1408
Byrrhidae: Byrrhinae: <i>Pedilophorus mixtus</i> Lea, 1907	39	8	3	39.1	0.3776
Chrysomelidae: Galerucinae: <i>Arsipoda variegata</i> (Westwood, 1838)	53	30	2	53.0	0.1936
Average IV's	53.3	15.4	5.4	53.5	

¹ *Decilaus lateralis* (Curculionidae) was not common enough to be included in the indicator species comparison of mature and young forest (Chapter 5) that identified mature forest characteristic species.

Indicator Species Analysis (Table 4) revealed the species-specific edge responses of beetles to the three edge zones: Firebreak (-10 m, -5 m and 1 m plots), Edge (5 m and 10 m), and Interior (25 m, 50 m and 100 m) forest. Beetle species that had previously been designated as characteristic of mature or young forest (Chapter 5) all showed trends in Indicator Value (IV) related to the edge zones. Mature forest characteristic species were all of maximum IV in Interior forest. Four species, *Choleva* TFIC sp 01 (Leiodidae), *Decilaus nigronotatus*, *D. lateralis* and *D. striatus* (all Curculionidae), were identified as indicator species characteristic of mature forest interior. In contrast, young forest characteristic species all attained maximum IV in Firebreak habitat. With the exception of *Rybaxis parvidens* (Staphylinidae), (which was only collected in Firebreak traps), species characteristic of young forest were of intermediate IV in Edge habitat and lowest IV in Interior forest habitat. One species, *Anabaxis* CHANDLER 'Type 1' (Staphylinidae) was identified as a mature forest avoiding species. Beetle species found in Chapter 5 to not be characteristic of either mature or young forest showed no general trends in Indicator Value in relation to edge response zones: 11 species attained greatest IV in Edge habitat and 8 species each in Firebreak and Interior habitat (species specific data not presented). No species were identified as being characteristic of the Edge zone.

Discussion

Edge effects are important to native forest management because silvicultural practices can result in fragmentation and alteration of ecosystem dynamics. Quantifying these phenomena for invertebrates is crucial, since their small size and cryptic habits could mean that detrimental changes go unnoticed, posing an extinction risk for sensitive species (Bryant and Jackson, 1999; Meggs and Munks,

2003). We have shown that ground-dwelling beetles in wet eucalypt forest respond to habitat edges between mature and recently clearfelled and regenerated forest. The species composition of beetles changed gradually with distance from the edge. Edge effects extended between 10 m and 25 m into mature forest and the beetle assemblage was estimated to be 95% similar to interior forest at approximately 22 m from the edge, although 95% confidence intervals of 2-100% indicate high uncertainty associated with this latter prediction. As predicted, species characteristic of mature forest were most common in unlogged forest interior while species characteristic of young logging regeneration were most common in the coupe firebreak, corroborating the findings of Chapter 5. The transition in the species assemblage with distance from the edge appeared to be dominated by changing abundances of species characteristic of mature and young forest. Four species, *Choleva* TFIC sp 01 (Leiodidae), *Decilaus nigronotatus*, *D. lateralis* and *D. striatus* (all Curculionidae), were identified as indicator species characteristic of mature forest interior, suggesting that at least 50% of mature forest species avoided edges.

Species not characteristic of either stand age did not show strong edge responses. Like Spence *et al.* (1996) and Heliölä *et al.* (2001), we did not document any species characteristic of the habitat edge, possibly because beetles are not adapted to such unnaturally abrupt transitions in this forest. Abrupt edges are not really a characteristic of the wet eucalypt forest environment, since natural successional edges created by wildfire boundaries would be less distinct. Unlike some northern hemisphere forests (Schowalter *et al.*, 1997; Lindenmayer and Franklin, 2002), large canopy gaps resulting from windthrow, insects and pathogens are rare in this forest type. Thus it is possible that edge specialist species have not evolved, and so are not available to use the distinctive conditions created at logging coupe edges. However, preferences by some species for the edge are possible, since

11 of 41 common species attained their maximum indicator value at the edge. Edge-attraction, deeper DEIs for certain especially edge-sensitive species, or idiosyncratic responses by some species may not have been detected as significant due to the low power of single species analyses, and the indicator species analysis approach based on edge zones derived from community analyses.

Given that a reasonable proportion of the more commonly trapped beetles showed a preference for particular successional ages (Chapter 5) and patterns of edge avoidance (this study), edge avoiding behaviour and sensitivity to forest management are also likely to be shown by a similar proportion of the hundreds of ground-dwelling beetle species present in this habitat. Since rare species are potentially more sensitive to fragmentation and suffer inherently greater extinction risk (Didham et al., 1998b; Davies et al., 2004), the findings of this study should be considered in the broader sense of potential risks to the entire ground-dwelling beetle community.

Most of the commonly collected species were present on both sides of the habitat edge, including species characteristic of mature, interior forest habitat (*Decilaus lateralis* is an exception). This demonstrates a degree of edge permeability or leakiness (Stamps et al., 1987; Dangerfield et al., 2003), possibly related to a transition in habitat quality that extends beyond the edge (Ries et al., 2004). Alternatively, the presence of some individuals of species characteristic of interior forest at the edge and firebreak could mean that the edge is acting as a population sink (Didham, 1997).

The narrow DEI recorded for beetles in this study compared to other similar studies (e.g. Didham, 1997; Davies et al., 2001; Grove and Yaxley, 2005), and the presence of some interior forest beetles up to and over the edge, could also relate to adaptation to the characteristically patchy nature of Tasmanian wet eucalypt forest under the natural fire regime (Harper and MacDonald, 2001; Baker et al., 2004).

Beetles may also be better adapted to edges between two successional ages within one forest system than to edges between forest and land cleared for agriculture (Didham, 1997), or converted to *Pinus radiata* plantation (Davies et al., 2001). DEI may not necessarily be maximised at the largely east-facing coupe edges in this study (Ries et al., 2004), although the influence of orientation might be expected to diminish for higher trophic levels (Ries et al., 2004).

Since some of the mature forest characteristic species were collected occasionally in 33-year old regeneration (Baker, 2000; Chapter 5), it seems likely that the degree of influence of edge effects may diminish as the regeneration ages and the contrast in conditions (e.g. vegetation height) becomes less severe (Matlack, 1994; Kapos et al., 1997; Forestry Tasmania, 1998; Michaels, 1999). However, Westphalen (2003) found that vegetation and microclimate edge effects had not dissipated 15 years following clearfelling in Tasmanian wet forest. Wind-throw of trees and edge creep may be relevant in the short to medium term (Kapos et al., 1997; Westphalen, 2003). Further research into temporal effects of edge age over 90-year harvesting rotations would be worthwhile.

Potentially confounding effects of variation in edge aspect, slope, age and escaped regeneration burns did not appear to interfere with quantification of edge effects, which were consistent amongst study sites. Further research, with greater replication, would be needed to specifically investigate the influence of these factors on edge penetration for beetles, and to determine whether edge penetration is greater in some conditions than that predicted by this study.

Differences in beetle assemblages among the four study sites were greater than differences along the edge-interior gradient. Other studies have found high beta diversity for beetles in this ecosystem (Baker et al., 2004; Bar-Ness et al., 2006; Chapter 2; Chapter 4), with site differences also outweighing riparian influences on

ground-dwelling beetles near small streams (Chapter 3). The mechanisms behind this high turnover among sites need further exploration, but probably relate in part to previous fire history (Gilbert, 1959; Gilbert, 1963).

Although challenging, it would be interesting to investigate the mechanisms that underlie species specific edge responses; e.g. ecological flows, access to resources, and species interactions (Ries et al., 2004). Correlation of young and mature forest characteristic species with coupe firebreak and mature forest interior areas respectively, suggest that resource mapping may be an important mechanism in this case. Currently, however, very little is understood about these aspects of beetle ecology in Tasmanian forest. Correlations of habitat structural variables in this study were uninformative (S. Baker, unpublished data), although Yee (2005) has demonstrated that some beetle species specialise on large fallen logs and their associated fungal decay communities. The four species characteristic of mature forest interior identified in this study were found by Yee (2005) to be saproxylic, suggesting that proximity to suitable rotting logs may underlie these species' edge responses. Tasmanian ground-dwelling beetles have also been found to respond to natural environmental gradients, in relation to distance from streams (Chapter 3; Chapter 4), suggesting that beetles' edge response might be partially related to subtle changes in environmental conditions. However, since Westphalen (2003) generally found edge penetration of less than 10 m for vegetation and microclimate in the same habitat type, it is probably not the whole explanation. Further research documenting the habitat requirements and dispersal abilities of Tasmanian beetles would assist in understanding the specific mechanisms underlying the edge-response of different species. A concurrent study will also allow estimation of edge effects into riparian habitat (S. Baker, unpublished data).

Area and isolation effects are known to affect forest biodiversity elsewhere (Bierregaard et al., 1992; Davies and Margules, 1998; Didham et al., 1998a)(Bierregaard et al., 1992; Davies and Margules, 1998; Didham et al., 1998a). Didham (1997) suggested that area effects may be a stronger determinant of beetle species composition than edge effects, and concluded that Amazonian forest fragments needed to be greater than 100 hectares to host an intact fauna. By contrast, the beetle community in Australian eucalypt fragments surrounded by a pine matrix appeared to be more strongly influenced by edge effects than patch area (Davies et al., 2001). These contrasting results from other forest systems emphasise the need for future research to investigate the importance of habitat area for biodiversity conservation in managed forest landscapes.

Knowledge of edge penetration distance can assist evaluation of different silvicultural options for maintaining core habitat (Laurance, 1991; Laurance and Yensen, 1991; Sisk and Margules, 1993). DEI could be incorporated with GIS tools to allow calculation of the exact edge to interior ratios of coupes to assess the broader impacts of fragmentation in Tasmania's managed wet forests. The influence of an estimated 22 m edge penetration into non-riparian habitats will vary amongst silvicultural practices. For example, for mature forest patches greater than approximately 20 ha, the proportion of interior forest may be greater than 80%, depending on the patch shape (Laurance and Yensen, 1991). Most clearfell logging areas are >20 ha, and are unlikely to be completely surrounded by young regeneration forest. Therefore, stands regenerated with this silvicultural regime would provide core habitat for populations of edge-avoiding mature forest ground-dwelling beetles, assuming a long enough silvicultural cycle and retention of suitable woody debris. Edge effects may be more significant in the small patches retained as part of alternative silvicultural systems (see Hickey et al., 2001). For example, while

0.5-1 hectare patches retained in aggregated retention might contain a small percentage of core area, approximately 0.1 hectare understorey islands would be entirely edge affected. It should, however, be acknowledged that variable retention silviculture is not intended to provide all the ecological characteristics and habitat value of mature forest in the retained clumps. They are instead considered important in providing habitat structure and complexity within the coupe overall, while still having habitat value for some mature forest species. One-hundred meter wide wildlife habitat strips (Forest Practices Board, 2000) adjacent to young regeneration in non-riparian habitats probably contain a little over 50% interior forest for ground-dwelling beetles.

This study has shown that edge effects are acting on ground-dwelling beetles in managed Tasmanian wet eucalypt forest, and approximately 50% of mature forest species are specialised to forest interior. Many beetle species are also patchily distributed, of potentially low dispersal ability, and sensitive to local habitat conditions, all of which will additionally affect their response to forestry operations. Edge and fragmentation effects are key processes impacting forest biodiversity. Their study, and input into forest management planning, is fundamental to biodiversity conservation in managed forests.

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Chapter 7

Response of ground-dwelling beetles across logging coupe edges into riparian buffers

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Preface: This chapter investigates edge effects on beetles in streamside reserves.

Data from riparian areas in interior forest are used for reference, since edge effects and riparian influences are both acting on beetles in this habitat. Penetration of edge effects are compared to Chapter 6 which explored non-riparian edges.

Abstract

Streamside buffers can provide important habitat reservation in forest landscapes subject to logging. Depending on the width of streamside reserves, edge effects have the potential to compromise their effectiveness for terrestrial conservation, yet edge effects into riparian environments have rarely been assessed. It would be unwise to assume that edge effects act in the same way at streamside reserves as at the edges of non-riparian logging coupes, since interactions with riparian influences may create unique edge conditions. In this study we assess edge effects on ground dwelling beetles at four sites, using transects of pitfall traps between recently regenerated logging coupe edges and streams in streamside reserves. Edge effects were found to extend further into riparian habitat in this study than into non-riparian habitat at the same sites from a concurrent study. Edge effects extended as far as the stream in most cases (23-65 m). These results indicate that streamside reserves and wildlife habitat strips located in riparian areas do not contain ground dwelling beetle habitat comparable to riparian areas away from the influences of nearby clearfelling. Wider habitat strips are recommended to provide effective habitat for edge avoiding mature forest species.

Key words: Coleoptera, invertebrates, riparian, buffers, clearfelling.

Introduction

Streamside reserves (buffers) are widely applied in forestry areas worldwide. Although their primary role is usually the protection of aquatic values, they are also an important component of the terrestrial reserve system, potentially providing habitat and landscape linkages for species not suited to the conditions in harvested areas and young regeneration (Lindenmayer and Franklin 2002). In Tasmania, Australia, logging operations around permanent streams in catchments exceeding 50 ha require a buffer of uncut forest extending a minimum of 20 m from the streams, with requirements for ≥ 30 m buffers in larger catchments exceeding 100 hectares (Forest Practices Board 2000). The conservation value of streamside reserves for terrestrial wildlife may depend on the degree to which habitat conditions equate to those in undisturbed forest, with edge and area effects being key factors that could compromise their utility for some species (Soulé and Gilpin 1991, Didham et al. 1998, Hylander et al. 2002). Streamside reserves 20-30 m either side of streams have the potential to be mostly or entirely edge-affected for some forest-inhabiting species. A Tasmanian study found significant impacts of logging on aquatic invertebrates and their stream habitat when streamside buffer widths were <30 m (Davies and Nelson 1994), suggesting that impacts on the terrestrial environment in buffers might also be expected. Edge effects on ground-dwelling beetles are estimated to extend approximately 22 m into non-riparian coupe edges in Tasmanian wet eucalypt forest (Chapter 6). A key question is whether depth of edge influence (DEI) (Ries et al. 2004) into riparian habitats differs from that into other edge types.

Ground-dwelling beetles in Tasmanian wet eucalypt forest are numerous and speciose (Baker et al. 2004). Varied life histories, trophic levels, dispersal abilities and habitat requirements mean that the responses of beetles to forest management are

species specific (Lawrence and Britton 1994, Davies et al. 2000). As well as estimating edge effects into non-riparian habitats, studies conducted concurrently with this one also found that beetles respond to riparian influences (Chapters 3 and 4) and different assemblages occur in young logging regeneration to mature unlogged forest (Chapter 5). Since beetle assemblages in young logging regeneration differed substantially from those in mature unlogged forest (Chapter 5), streamside reserves have the potential to provide important habitat reservation for mature forest beetles. However, populations of edge-avoiding mature forest species (Chapter 6) may suffer if too great a proportion of these reserves are edge-effected.

It is well recognised that DEI differs among edge types, e.g. with edge aspect, structure, age, or with the habitat type of the modified landscape (Sisk and Margules 1993, Dignan and Bren 2003a, Ries, et al. 2004). It therefore seems surprising that little or no attention has been paid to the potential for DEI to differ between edges into streamside riparian habitat compared to non-riparian forest (but see Davies and Margules 1998). This is despite the frequent use of streamside buffers as coupe boundaries in managed forests and as corridors along streams and rivers in other landscapes such as farmland. Since ground-dwelling beetles have been found to respond to riparian conditions (Chapters 3 and 4), the potential exists for interactions between edge and riparian influences to produce a distinct edge response for beetles, possibly associated with changes to riparian microclimatic conditions. Streams and rivers may also form natural edges, especially for some ground dwelling beetle species that never or only occasionally fly for dispersal (Michaels and McQuillan 1995), and for which streams may form partial barriers.

Streams play an important role in influencing local microclimatic conditions. Unharvested riparian areas are naturally characterised by gradients in air and soil temperature, relative humidity (Brososke et al. 1997) and light levels (Dignan and

Bren 2003b); wind speed may also be lower in valleys (Brososke, et al. 1997).

These same factors also show gradients in response to edge effects (Matlack 1993, Chen et al. 1995, Dignan and Bren 2003b, Westphalen 2003). Riparian areas may be burnt less severely in wildfires than adjacent slope forests because of moister fuel conditions and the tendency for fires to burn with greater severity upslope than downslope (Luke and McArthur 1978, Ashton and Attiwill 1994).

The aims of this study were to assess the influence of edge effects on ground-dwelling beetles in streamside (riparian) reserves, and compare the depth of edge influence between streamside reserve and nearby non-riparian edges. The present study of streamside reserve edges was conducted simultaneously, and at the same four sites, as the investigation of edge effects into non-riparian habitats (Chapter 6), thus enabling direct comparisons to be made. The streamside reserves explored in this study have only been affected by logging on one side of the streams. This allows us to quantify edge effects on beetles in streamside reserves without confounding with area effects (*sensu* Lovejoy et al. 1986).

Methods

Study Sites

We conducted our study in wet eucalypt forest approximately 60 km WSW of Hobart, Tasmania, Australia. This forest type is dominated by *Eucalyptus obliqua* with an understorey of rainforest and sclerophyllous species. Annual rainfall in the region is approximately 1,300 mm, and headwater streams are common landscape features. Four study areas were used (Table 1); one site each are named after their locations in the Picton and Kermadie River valleys, and two sites in the Huon River valley are named Manuka and Warra after the nearest roads. Each study area was

centred on a recently (within 1 –5 years) clearfelled and regenerated logging coupe (Chapter 5). Clearfell-burn and sow has been the main silvicultural system used in wet eucalypt forest since the 1960s. Approximately 10-15 m wide firebreaks were mechanically cleared along the inner edge of coupe boundaries to protect adjacent unlogged forest from the high intensity regeneration burn (Westphalen 2003).

Regeneration burns do occasionally escape beyond the bounds of the harvested area, and penetrated short distances into the streamside reserves at the Picton and Warra sites (Table 1). In practice, the widths of streamside reserves vary both within and between sites. The streamside reserve edges are usually located as one of the coupe boundaries since the risk of the fire escaping increases if regeneration burns are concurrent on both sides of a reserve.

Table 1. Characteristics of study sites and edge transects.

	Picton	Warra	Manuka	Kermadie
<i>Sites</i>				
Forestry Tasmania coupe numbers	PC024A	WR011B	WR008B	KD022H
Edge relative to logging coupe	S	N	E	E
Elevation	100 m	380 m	130 m	300 m
Soil derivation	sandstone	dolerite	dolerite	dolerite
Location	43°7'S 146°42'E	43°3'S 146°42'E	43°6'S 146°41'E	43°13'S 146°53'E
<i>Transects</i>				
Distances from edge to stream (m)	62, 65, 95	47, 50, 56	25, 23, 39	29, 45, 25
Penetration of regen. burn (m)	5, 0, 10	0, 10, 28	–	–

At each site, one of the coupe boundaries was adjacent to a streamside reserve, while other coupe boundaries were either roads or non-riparian mature forest. This study investigated edge effects into the streamside reserves. Concurrent studies also quantified edge effects at one of the non-riparian coupe edges at each site (Chapter 6), compared beetle assemblages in mature forest away from environmental gradients to the logging coupe interiors (Chapter 5), and quantified riparian effects at nearby unharvested headwater streams (Chapters 3 and 4). These studies, described in detail elsewhere, provide reference information for the present study. In particular, data from nearby control streams are utilized here. The control streams were from adjacent catchments, and were of similar elevation, catchment sizes and vegetation communities.

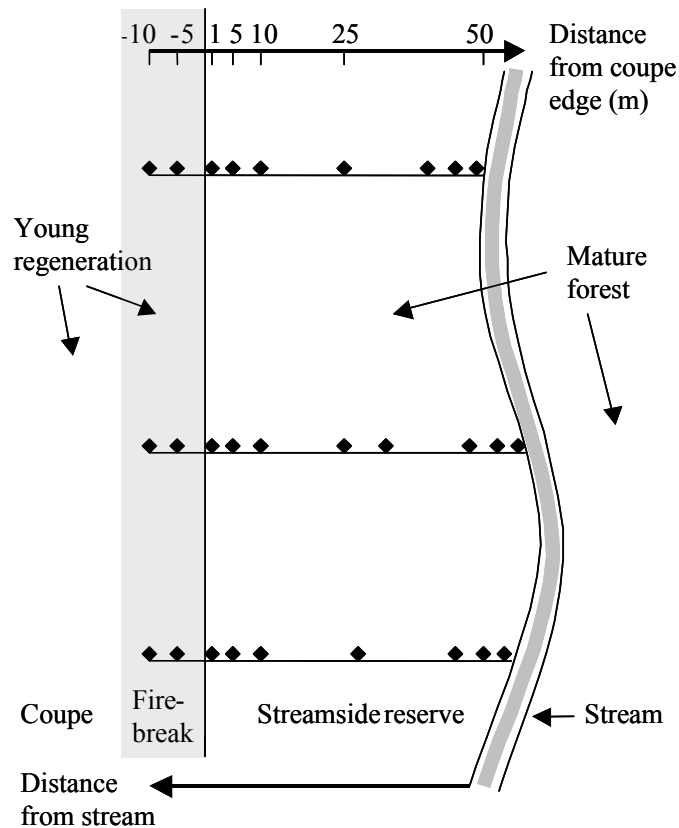
Sampling of Beetles

Ground-dwelling beetles were collected with pitfall traps consisting of 7.5 cm diameter plastic drinking cups inserted in PVC downpipe sleeves dug into the soil. Ethylene glycol (antifreeze) was used as preservative. A plastic lid was held in place above each trap with three wooden sticks to protect traps from rainfall and disturbance by vertebrates.

Three transects were randomly positioned along the length of the streamside reserve at each study site (Figure 1). Transects of traps crossed the coupe edges into streamside reserves and extended as far as the streams. The transect lengths differed both within and among sites depending on streamside buffer widths. However, traps were placed at fixed distances from both the coupe edges and from the streams to assist in disentangling the confounding influences of these two environmental gradients acting in opposite directions. Transects were positioned at right angles to the streams and coupe edges. The transect lengths (32–104 m) and the number of

Figure 1. Stylised representation of the layout of transects at streamside reserves.

Diamonds indicate the position of a pitfall trap. The number of traps and their position within transects varies depending on the distance between the coupe edge and the stream. Within the streamside reserves, traps are located at the following distances from both the coupe edges and the streams: 1 m, 5 m, 10 m, 25 m and 50 m (Picton and Warra sites only).



traps in transects (8–11) varied depending on the width of the streamside reserve at each location (Table 1). Within transects, traps were positioned at distances 5 m and 10 m into the coupe/firebreak (hereafter –5 m and –10 m), and 1 m, 5 m, 10 m, 25 m (all sites), and 50 m (Picton and Warra sites only) from both the coupe edge and

stream-bank in mature forest. Distance was measured along the ground rather than in the horizontal plane, since that was considered more relevant to ground-dwelling invertebrates. Where applicable, a single trap was used to represent both a distance from the edge and from the stream; in some cases ≥ 10 m from coupe edges, distances within 3 m were used to represent exact distances and thus reduce the numbers of traps. For transects slightly shorter than 25 m or 50 m (Table 1), traps within 3 m of these distances were included in analyses.

A similar transect design was employed at the four control streams away from logging coupes. Three transects of traps were randomly positioned along the length of each stream. Transects were at right angles to the stream, and traps were located at distances 1 m, 5 m, 10 m, 25 m, 50 m and 100 m from streams.

Pitfall traps were closed for at least three weeks before trapping to avoid digging-in effects (Greenslade 1964). Traps were operated for three separate one-month periods: winter (June – July 2001), spring (October – November 2001) and summer/autumn (February – March 2002). All beetles were removed and sorted to family and morphospecies based on external morphology (Oliver and Beattie 1996) using keys to family in Lawrence and Britton (1994) and Lawrence *et al.* (1999). Taxonomic knowledge of many beetle families is scarce, and identification to taxonomic species was not possible for all morphospecies. Species identifications were made by reference to the Tasmanian Forest Insect Collection at Forestry Tasmania, where the reference collection will be deposited on completion of ongoing studies.

Analyses

There is the potential for ecological patterns to arise from spatial autocorrelation or pitfall trap depletion, given that the trial design involves unequal distances between the traps within transects. These phenomena were screened for, using control transects in mature forest away from known environmental gradients, with trap distances 1 m, 5 m, 10 m, 25 m, 50 m and 100 m from random starting points (Chapter 2). Autocorrelation and depletion did not create detectable species assemblage patterns or affect abundance or species richness of beetles (Chapter 2). Data from the three trapping periods were pooled after testing to ensure that edge penetration did not shift seasonally (Appendix 4). Rare species (those of abundance less than 0.5% of the total abundance or recorded only from single samples) were removed from datasets for statistical analyses.

Initially, permutational multivariate ANOVA (NPMANOVA, Anderson 2001, Anderson 2003b) was conducted to test for distance and site effects, and their interaction, on beetle assemblages. To balance the design, data from the following distances from edges were used from all sites: -10 m, -5 m, 1 m, 5 m, 10 m and 25 m. We considered this justified since the edge transition zone was ≤ 25 m from non-riparian edges (Chapter 6). This dataset included 1,184 beetles from 26 morphospecies. This and subsequent NPMANOVA analyses were conducted on square-root transformed abundance data using Bray-Curtis dissimilarities and 9999 unrestricted random permutations of the raw data, with the three transects at each site considered replicates. Sites and distances were considered fixed effects. Sites were considered as a fixed effect since the number of sites that met our selection criteria was limited in the Southern forests, and it seemed legitimate to examine differences between sites statistically to generate further hypotheses about differences in behaviour between the sites.

NPMANOVA analyses for the effect of distance were also conducted separately for the four sites. The six distances from edge used in the Site x Distance analysis were again used for all sites, with the additional inclusion of 50 m distance category for Picton and Warra sites where the streamside reserves were wider. Datasets were: Picton, 494 beetles from 40 morphospecies; Warra, 519 beetles from 22 morphospecies; Manuka, 252 beetles from 35 morphospecies; Kermandie, 468 beetles from 35 morphospecies. There was insufficient power to assess significance of pairwise comparisons of distances with NPMANOVA. Constrained CAP (Canonical Analysis of Principal Coordinates) ordinations (Anderson 2003a, Anderson and Willis 2003) of beetle assemblages in relation to distance from edges were conducted individually for each site, based on the same distance categories used in site-specific NPMANOVA tests. CAP analyses used square-root transformed abundance data and Bray-Curtis dissimilarities. CAP presents the ordination axes that best describe separation amongst pre-defined treatments, in this case distance from edge categories. Vectors are plotted for species that were correlated with either of the first two canonical axes with $r > |0.5|$.

Riparian influences are site specific, probably disappearing after approximately 10 m at many headwater streams (Chapters 3 and 4). In the absence of riparian indicator species (Chapters 3 and 4, Appendix 3), other approaches were taken to ascertain whether gradients in beetle assemblages approaching the streams might, over some of the gradient, be caused solely by riparian effects, rather than by edge effects or a combination of edge and riparian influences. Patterns in relation to the edge were observed for beetle species identified in the related studies as edge avoiding mature forest characteristic species (from non-riparian transects), and mature forest and young regeneration characteristic species (Chapter 5). We also compared beetle assemblages from the immediate riparian area (1 m, 5 m, and 10 m

from streams) in streamside reserves to the equivalent zone at the control stream sites. NPMANOVA compared streamside reserve-riparian, control stream-riparian, and streamside reserve-edge (1 m, 5 m, and 10 m from edge) areas. This design concurrently tests whether streamside reserve riparian areas differ from control riparian areas (i.e. whether they are still edge effected), and whether riparian effects on ground-dwelling beetles are equivalent to those of artificially created habitat edges (streams are natural edges).

The NPMANOVA model tests Site, Zone (streamside reserve-edge, streamside reserve-riparian, control stream-riparian), and their interaction. Pairwise *a posteriori* comparisons assess zone effects within each site. Some turnover in beetle assemblages occurs at the scale of adjacent catchments (Chapters 3 and 5). Therefore, we also conducted a constrained CAP ordination with two *a priori* groups; streamside reserve-riparian and control stream-riparian. This illustrates overall patterns with respect to treatment differences, without emphasising site differences that could identify patterns due to turnover rather than edge effects, as in NPMANOVA.

Results

Edge Effects into Streamside Reserves

A total of 2,843 beetles were collected from the edge transects at streamside reserves. The edge responses of beetle assemblages responded to distance from edge differently amongst streamside reserve sites (significant Site x Distance interaction in NPMANOVA; Table 2). Subsequent analyses therefore investigated the edge response on a site-by-site basis.

NPMANOVA found distance from edge significantly influenced beetle assemblages for Picton, Warra and Manuka study sites, but not for the Kermandie

site (Table 3). Transitions in beetle assemblages in relation to distance from coupe edges were visible at all study sites, although beetle species that were associated with interior areas of reserves towards the streams varied amongst the sites (Figure 2).

Table 2. Results of NPMANOVA analysis for the response of ground-dwelling beetle assemblages to study sites and distance from coupe edges.

Source	d.f.	MS	F	<i>P</i> -value
Site	3	29498.46	13.6608	0.0001
Distance	5	4401.728	2.0385	0.0003
Site x Distance	15	3254.788	1.5073	0.0012
Residual	48	2159.35		

Table 3. Results of NPMANOVA analysis for the affect of the distance from coupe edge on beetle assemblages at streamside reserve edges at four study sites.

Site	MS (Distance)	MS (Residual)	F	<i>P</i> -value
Picton ¹	4292.484	2884.385	1.4882	0.0361
Warra ¹	4291.398	2815.099	1.5244	0.0274
Manuka ²	4670.086	2523.558	1.8506	0.0020
Kermandie ²	2647.731	2439.764	1.0852	0.3409

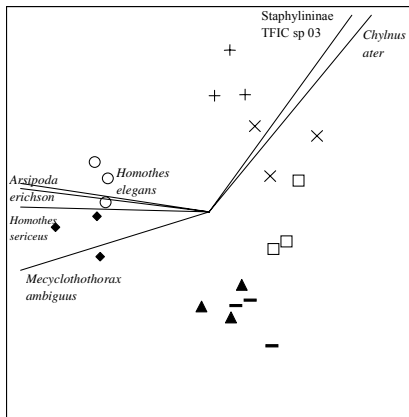
¹ d.f.: Distance = 6, Residual = 14; ² d.f.: Distance = 5, Residual = 12

For the Kermandie site, assemblages at two of the three plots 25 m from the edge (i.e., the distance category closest to the stream) were clustered with firebreak assemblages towards the right on the horizontal axis. Because of this, the edge response was less evident than at the other three sites, as indicated by the non-significance of NPMANOVA. At Kermandie, a transition along the vertical axis for

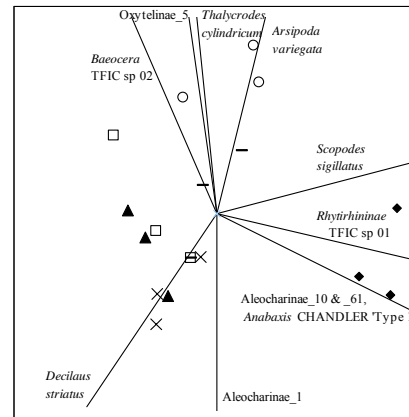
1 m, 5 m and 10 m plots was more consistent with the transitions apparent at the other sites. None of the three beetle species associated with the ordination are characteristic of mature forest interior. However, Aleocharinae_1 (Staphylinidae) and *Austronemadus* TFIC sp 03 (Leiodidae) are associated with the cluster of firebreak and 25 m plots, and these species both have strong preferences for mature forest over young logging regeneration (Chapter 5).

Figure 2. Constrained ordinations of beetle assemblages in relation to distance from logging coupe edge at four study sites. Diamonds indicate plots 10 m into the coupe firebreak, circles indicate plots 5 m into the firebreak, dashes 1 m into unlogged forest, squares 5 m, triangles 10 m, crosses 25 m, and plus signs 50 m (Picton and Warra sites only).

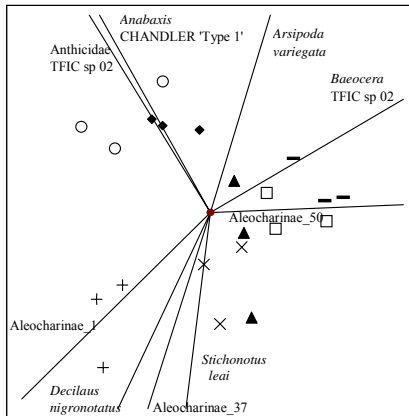
Picton



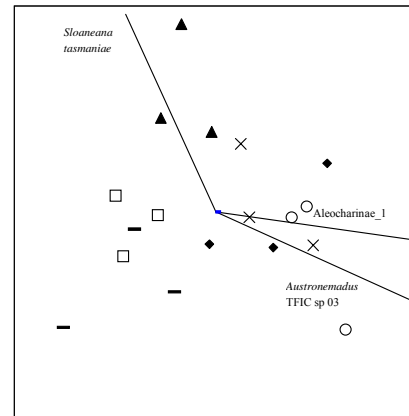
Manuka



Warra



Kermadie



At Picton, the beetle assemblages differed significantly with position along streamside-reserve edge transects. Firebreak plots were clearly separated from unlogged forest plots to the left along the horizontal axis, and two of the correlated species (*Mecyclothorax ambiguus* and *Homothus elegans*, both Carabidae) have preferences for young over mature forest (Chapter 5). Unlogged forest plots appear to follow a transition along the vertical axis, which is still apparent by 50 m from the edge, except that 10 m plots are most closely aligned with 1 m plots towards the bottom of the vertical axis. No species characteristic of mature forest were associated with the ordination.

At Warra, beetle assemblages in firebreak plots were distinct from those in unlogged forest, in this case to the top-left in the CAP ordination. These plots were correlated with the coupe and firebreak characteristic species *Anabaxis* CHANDLER ‘Type 1’ (Staphylinidae), and with Anthicidae TFIC sp 02 that also has an apparent preference for young forest (Chapter 5). A trend in assemblage composition from 1 m to 50 m in streamside reserves was apparent, tending diagonally towards the bottom and left of the plot. Forest at 50 m from the edge may be approaching interior forest conditions, based on association with the interior forest characteristic species *Decilaus nigronotatus* (Curculionidae). Aleocharinae_1 (characteristic of mature forest) is also correlated in this direction.

At Manuka, plots from 10 m into the firebreak were distinctly separated to the right of the horizontal axis. These plots were correlated with *Anabaxis* CHANDLER ‘Type 1’, a species characteristic of coupe and firebreak habitats. The remaining plots formed a series from those 5 m into the firebreak at the top, to those 25 m into the streamside reserve towards the bottom. The mature forest interior species *Decilaus striatus* (Curculionidae) is correlated in the direction of 25 m plots, as is Aleocharinae_1 (mature forest indicator).

Comparison with Riparian Control Areas

Beetles were also found to have site-specific responses to three zones: control stream-riparian, streamside reserve-riparian, and streamside reserve-edges (NPMANOVA analysis, Table 4). Pairwise comparisons showed highly significant differences for all sites in assemblages between control stream-riparian and streamside reserve-edge zones (Table 5). Differences between streamside reserve-riparian and streamside reserve-edge zones were also statistically significant at all sites, although marginally so in the case of Picton ($P = 0.0496$). These results indicate that beetle assemblages at coupe edges are distinct from the riparian zones of both streamside reserves and control streams. There is no evidence to suggest that edges have similar influence on beetles to riparian areas, including the Kermandie site where beetles assemblages at 25 m from edges were positioned close to those of firebreaks in the ordination (Figure 2). In contrast, there was substantial site-to-site variation in the significance of the comparison between streamside reserve-riparian and control stream-riparian assemblages: differences were highly significant for Kermandie and Manuka sites, marginally significant at Picton and non-significant at Warra (Table 5).

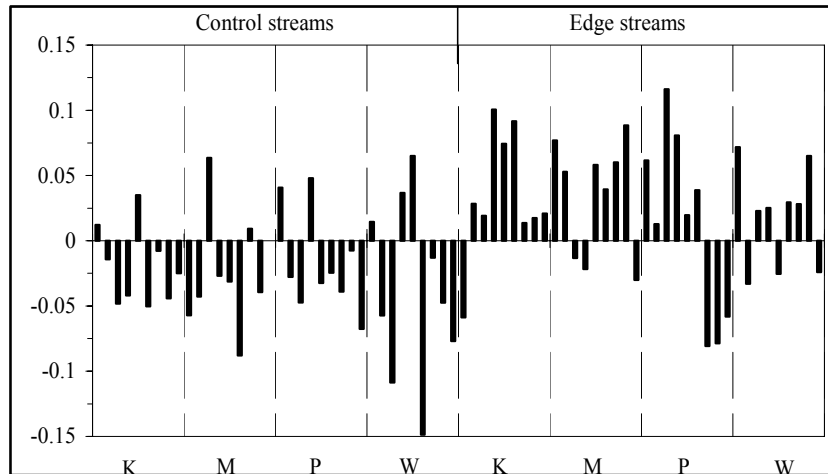
Table 4. Results of NPMANOVA testing for differences between the three Zones, control stream-riparian, streamside reserve-riparian, and streamside reserve-edge, at four sites.

Source	d.f.	MS	F	<i>P</i> -value
Site	3	11863.04	4.5334	0.0001
Zone	2	12759.71	4.8761	0.0001
Site x Zone	6	5533.724	2.1147	0.0001
Residual	96	2616.802		

Table 5. Pairwise comparisons for Zone effects within study sites. CS indicates control stream-riparian; SR-r, streamside reserve-riparian; and SR-e, streamside reserve-edge zones.

Comparison	Kermandie		Manuka		Picton		Warra	
	t	P-value	t	P-value	t	P-value	t	P-value
CS-r vs. SR-r	1.4597	0.0171	1.5386	0.0133	1.3839	0.0492	1.0491	0.3700
CS-r vs. SR-e	1.7201	0.0004	1.5589	0.0075	1.9439	0.0001	1.9867	0.0002
SR-r vs. SR-e	1.8215	0.0004	1.9748	0.0006	1.3459	0.0496	2.0324	0.0004

Figure 3. Axis scores from a one-dimensional CAP ordination comparing beetle assemblages from streamside reserve-riparian and control stream-riparian zones. For each site the axis scores are presented in order for 1 m, 5 m, 10 m distances from stream for each transect in turn. ‘K’ indicates Kermandie; ‘M’, Manuka; ‘P’, Picton; and ‘W’, Warra.



The constrained ordination comparing assemblages between streamside reserve-riparian and control stream-riparian habitats (Figure 3) mostly supported the

results of NPMANOVA contrasts, but provided additional insights for Picton and Warra sites. At all four sites, the majority of control stream-riparian plots had negative canonical axis scores while the majority of streamside reserve-riparian plots had positive scores. Exceptions to this trend (approximately one-quarter of plots) were mostly scattered across sites, transects and the control versus riparian zones. Of interest were negative axis scores from all three plots in the third transect at Picton when all other plots at this site had positive axis scores. This particular transect extended 95 m from the logging coupe edge, 30 m further than the next-widest streamside reserve width assessed. The riparian beetle assemblages in this case appears to be equivalent to those in control stream riparian areas, but riparian areas in other streamside reserve transects at all sites are probably still in edge transition habitat. We therefore interpret these results as indicating that streamside reserves may still be subject to edge effects as far as 65 m from the coupe edge, but that edge effects have dissipated beyond approximately 85 m.

Discussion

This study demonstrates that edge effects alter the assemblages of beetles in streamside reserves adjacent to recently clearfelled and regenerated wet eucalypt forest. Streamside reserves differ from non-riparian coupe edges in that the forest is subject to the separate influences of edge and riparian effects. The potential for interaction between these two environmental gradients complicates efforts to disentangle them in the absence of riparian indicator species. However, our analyses suggest that the transitions observed in beetle community composition from the edge to the stream were caused, at least partially, by edge effects. Two lines of evidence support this contention. Firstly, beetle assemblages differed in composition between

streamside reserves and control streams within the 10 m zone closest to the stream. Secondly, mature forest and interior forest specialist beetles were correlated in ordinations with the locations of traps that were furthest from the edge (except at Picton), while species characteristic of young forest were correlated with firebreak traps (except at Kermadie). Correlation of the curculionids *Decilaus nigronatus* (Lea, 1913) with 50 m plots at Warra and *D. striatus* (Lea, 1913) with 25 m plots at Manuka, further suggests that the habitat conditions at these distances were becoming suitable for some mature forest interior characteristic species, even though comparisons with riparian control areas indicated that these zones (especially at Manuka) were still exposed to edge effects. This study took place in forest where logging had only occurred on one side of the streams, thus providing intact source populations of interior forest beetle species (Didham 1997). The long-term survival of interior forest sensitive species in streamside reserves once logging has occurred on both sides is more questionable, and will be investigated in another study (Chapter 8).

Interestingly, the response of beetles at streamside reserve edges differed amongst sites, in contrast to the non-riparian edges of the same coupes where the response was more consistent, and estimated to extend approximately 22 m from the edges (Chapter 6). In streamside reserves, edge effects were estimated to extend over most or all of the streamside areas, ranging from 23-65 m width, with the exception of one very wide reserve (95 m). Because the study design consisted of transects extending only as far as the streams, we were unable to estimate fully the depth of edge influence, but these results suggest that streamside reserves may still be subject to edge effects as far as 65 m from the coupe edge, but that edge effects dissipate beyond approximately 85 m.

Site-to-site variation in edge effects in streamside reserves might relate to differing interactions with riparian conditions, because of variable transect widths between the edges and streams. Another possibility is that strength of riparian influences may also vary amongst the streams, as was found to be the case at control riparian areas (Chapters 3 and 4). Although the concurrent riparian study did not identify riparian or upslope specialist species, there is potential for some species to map onto specific habitats or resources (Ries, et al. 2004) in the riparian zone (e.g. microclimatic conditions, or the stream itself for beetles with terrestrial adult and aquatic larval stages (Gooderham and Tsyrlin 2002) or predatory terrestrial species that feed on aquatic invertebrates (Paetzold et al. 2005)). However, there was no consistency in the beetle species correlated with ordinations among the four sites, although most species associated with areas near the streams were also commonly collected from non-riparian habitat, and several of these were characteristic of interior or mature forest. Thus there is also no evidence from this study to suggest that specialised riparian beetles are responsible for assemblage patterning.

At the oldest of the four coupes, Kermandie, two of three plots 25 m from edges were positioned near firebreak plots in the ordination. However, NPMANOVA analysis found significant assemblage differences between the immediate edge and streamside zones, indicating that beetles were not responding to the stream in the same way as the coupe edge. At all sites, comparisons between streamside reserve-edges and streamside reserve-riparian beetle assemblages indicated very little overlap. Thus, although it is possible that small streams may have certain barrier or edge effects associated with them, they apparently create very different community patterning than the edges of logging coupes. This is not surprising for small streams where the canopy generally extends over the stream, and fallen logs provide some connectivity with the other stream bank. It would be interesting to investigate

whether lakes or rivers have natural edge effects for beetles (Harper and MacDonald 2001). However, the patterns in the transition zones at coupe edges were partly due to species which prefer young logging regeneration, and so natural landscape features are unlikely to generate similar edge-related beetle assemblages.

Disruption of riparian microclimatic gradients following harvesting seems to be a plausible explanation for the greater depth of edge influence (DEI) observed at streamside reserves than at non-riparian coupe edges. Microclimatic changes themselves may be more extreme at moister, more buffered riparian environments, although to our knowledge this has not previously been investigated. Clearfell harvesting of adjacent forest disrupts the natural microclimatic gradients in streamside reserves (Brosfokske, et al. 1997). In Douglas Fir-dominated forests, for example, 72 m wide buffers were insufficient to fully ameliorate changes to riparian air temperature resulting from edge creation (Dong et al. 1998). At non-riparian, wet forest coupe edges in Tasmania, microclimatic edge effects (temperature, vapour pressure deficit) generally dissipate after approximately 10 m into uncut forest, while changes in photosynthetically active radiation (PAR) were detectable up to 50 m (Westphalen 2003). Dignan and Bren (2003b) found increased light penetration as far as 70-100 m into streamside buffers in similar forest in Victoria. Soil and litter conditions in riparian areas may potentially relate to groundwater as well as to above-ground microclimatic conditions (Naiman et al. 2005). Streamflow generally peaks within three years of harvesting because of reduced evapotranspiration losses (Vertessey 1999), thus suggesting that water dynamics are likely to be different in riparian areas adjacent to recently harvested coupes compared to in unlogged forest.

The causal mechanisms behind the edge response of beetles are presently unknown, including the potentially important influence of edge orientation. In our study, it is not possible to definitively attribute the deeper penetration of edge effects

into streamside reserve edges over those observed in non-riparian edges to the influence of riparian conditions, since the sites differ in slope and orientation of streamside versus non-riparian edges (Ries, et al. 2004). Edge-affected beetle assemblages are probably responding to a combination of factors, including position along the gradient from riparian areas to ridges, and the site slope and aspect. Depth of edge influence was consistent among sites for non-riparian edges, which included downward slopes into mature forest at Manuka and Kermandie (unpublished data). Thus slope relative to the edge *per se* appears not to be an explanation for the deeper DEI into streamside edges. Escaped regeneration burns (Didham and Lawton 1999) also appear to be unrelated to deeper edge penetration into riparian than non-riparian edges since the depth of escaped burns were greater into non-riparian than riparian habitat at both the Picton and Warra sites where burns extended over the habitat boundary (Table 1 and Chapter 6).

Edge orientation is a possible explanation for the greater penetration of edge effects observed at the streamside reserve than at non-riparian edges, and merits further investigation. Except for a study of goldenrod ball gall insects (Confer and Orloff 1990), we are unaware of research into edge aspect affects on invertebrates; however, Ries et al. (2004) hypothesise that the influence of aspect is likely to diminish with higher trophic levels. Southern forest edges bordering open habitat should experience stronger edge effects in the southern hemisphere temperate zone because of increased exposure to sunlight (Dignan and Bren 2003a, Ries, et al. 2004). Additionally, western coupe edges in our region would experience the morning sun, and eastern edges would experience increased exposure to winds, since the dominant wind direction is from the west (Bureau of Meteorology wind frequency data from Warra). The streamside reserve edges examined here included two eastern coupe edges and one northern and one southern coupe edge. The non-

riparian edge study at the same four sites used three western and one eastern coupe edge. Based on edge orientation, the northern streamside reserve coupe edge at Warra would therefore be expected to have the narrowest edge penetration; however, like the other riparian edges, DEI exceeded that of the non-riparian coupe edges. Thus, while aspect may be part of the explanation, we contend that edge penetration on ground-dwelling beetles in wet forest is deeper into riparian than into slope habitats. An additional study in which riparian and non-riparian habitat edges are matched for aspect would be required to attribute the greater DEI to one or other explanation definitively. Combining such a study with assessment of microclimatic factors would be a major contribution towards designing ecologically sensitive buffers for forest management.

Acknowledgements

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Chapter 8

A comparison of ground-dwelling beetle assemblages in streamside reserves with those in unlogged wet eucalypt forest

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Preface: This chapter assesses whether beetle assemblages in streamside reserves that have been previously logged on both sides are comparable to those in mature forest interior habitat. The chapter is based on Trial 2 of the thesis, and is intended to validate predictions about reserve effectiveness made in Chapters 4 and 7. Indicator species for forest age (Chapter 5) and mature forest interior (Chapter 6) assist interpretation of results.

Abstract

Reservation of forest in riparian buffers is common practice in commercial forestry areas worldwide, potentially providing valuable habitat for biodiversity dependent on mature forest. However, the habitat value of narrow reserve corridors can be compromised by edge effects. We investigated the habitat value of streamside buffers in wet eucalypt forest for ground-dwelling beetles in Tasmania, Australia. Beetles were collected with pitfall traps in five replicates of four habitats: unlogged corridors of mature forest in streamside reserves (buffers) with clearfelled logging regeneration either side; continuous mature upslope forest; continuous mature riparian forest; and < 20-year-old logging regeneration. Streamside reserve widths on each side of the stream were on average 40 ± 6 m ($\pm 95\%$ CI) from reserve edge to stream. During a four-week trapping period in October-November 2002 6,530 beetles were collected. Beetle assemblages in logging regeneration differed substantially from those in the unlogged habitats including the streamside reserves. Streamside reserve assemblages nevertheless differed from those of the continuous unlogged areas (both riparian and upslope), with a greater preponderance of edge-tolerant mature forest species. Edge-avoiding mature forest specialist species may be disadvantaged in streamside reserves, and wider reserves would be required to provide habitat equivalent to continuous forest.

Key words: corridors, habitat, Coleoptera, forest management, indicator species

Introduction

Forestry activities such as clearfell logging are changing the age structure and patch dynamics of forest, with potentially negative consequences for forest biodiversity. Beetles from the forest floor have been shown to be sensitive to the regeneration age of the forest, with different beetle species assemblages inhabiting mature forest compared to young regeneration following clearfelling (Chapter 5). Unlike many European forests (e.g. Mönkkönen 1999), intensive forest management is relatively recent in Tasmania's commercial forest landscape, with clearfelling having been the predominant silvicultural regime in wet eucalypt forests only since the 1960s. Areas of old-growth forest are currently included in harvesting regions, and future planned management on 90-year rotations would prevent most such stands from achieving an old-growth stage. Careful landscape planning, and incorporating reserves of mature forest, have the potential to ameliorate effects of logging on forest biodiversity (Lindenmayer & Franklin 2002).

Streamside reserves (buffers) and wildlife habitat strips are important components of reserve networks, contributing mature forest habitat and connectivity across the landscape. The Tasmanian Forest Practices Code (Forest Practices Board 2000) prescribes streamside reserves of 20-30 m of uncut forest either side of streams in catchments exceeding 50 ha, chiefly to ensure the protection of aquatic values. Additionally, 100 m wide uncut wildlife habitat strips are to be provided every 3-5 km to provide landscape connectivity; these are currently predominantly aligned as widened streamside reserves, hence 'upslope' (non-riparian) habitat is relatively underrepresented. Yet the conservation value of reserve corridors may suffer because of ecological changes caused by edge effects (Hobbs 1992; Soulé & Gilpin 1991). Depending on the depth to which edge effects penetrate relative to the width of the

reserve, there is the risk that corridors will only function as edge habitat and host edge species (Niemelä 2001). This may be the case for ground-dwelling beetles inhabiting riparian corridors in Tasmanian wet eucalypt forest, since edge effects into streamside reserves have been estimated to extend as far as 65 m (Chapter 7). Ground-dwelling beetles have also been demonstrated to be sensitive to riparian influences in this forest type (Chapters 3 and 4), with lower abundance and possibly reduced species richness in some riparian areas, although common species do not appear to be specialized to either riparian or upslope habitat.

In boreal forest, corridors appear to be an intermediate habitat type between clearcuts and undisturbed forests for beetles and spiders (Henttonen et al. 1998, cited in Niemelä 2001) and land snails (Hylander et al. 2004), whilst they were found to provide effective habitat or dispersal routes for moth species associated with mature forest (Mönkkönen & Mutanen 2003). In wildlife habitat strips in northern Tasmanian damp forest, Grove and Yaxley (2005) also found that the assemblage composition of ground-dwelling beetles was intermediate between continuous forest and plantations. Results were more ambiguous in a study of carabids in southern Tasmanian wet forest (Taylor et al. 2000). Although abundance and richness responses are variable (Ries et al. 2004), edge effects and the colonization of corridors by some species typical of regeneration forest could inflate species richness and abundance in corridors (Davies et al. 2001; Driscoll & Weir 2005; Halme & Niemelä 1993). Forest interior specialists identified in previous research on edge effects (Chapter 6) may prove particularly useful in assessing corridor effectiveness (Hill 1995). Mönkkönen (1999) predicts that corridors will be most useful for species that require old forest but are not sensitive to edges.

These mixed results prompted the overall aim of this study: to assess whether streamside reserves support beetle assemblages equivalent to continuous unlogged

riparian and upslope areas, and to assess the suitability of such reserves for edge-sensitive versus edge-tolerant species. Based on the foregoing literature, we proposed the following hypotheses about ground-dwelling beetle assemblages within the interior of streamside reserves:

1. streamside reserve assemblages will differ from continuous mature riparian, continuous mature upslope, and young logging regeneration habitats;
2. such assemblages should be intermediate in composition between those of mature forest and logging regeneration habitats;
3. as a consequence, streamside reserves should have greater species richness than continuous mature riparian habitat; and
4. edge-avoiding mature forest indicator species should be disadvantaged in streamside reserves relative to continuous mature upslope and riparian habitats.

Methods

Study Sites and Collection of Beetles

The study was conducted in wet *Eucalyptus obliqua* dominated forest in the Picton River Valley in southern Tasmania, Australia. The study was restricted to an approximately 5 x 8 km locality in order to minimize the influences of site turnover on beetle assemblage composition (see Baker et al. 2004). This locality has been managed for wood production with clearfelling since the 1970s, and is a mosaic of logged areas and uncut mature eucalypt forest. Areas logged prior to the adoption of streamside reserves in the 1980s were not included in the present study. Beetles were collected from five replicates of each of four habitat types (Table 1): (1) unlogged mature riparian forest in streamside reserve corridors with clearfelled logging regeneration either side, (2) continuous mature upslope forest, (3) continuous mature

riparian forest, (4) clearfelled logging regeneration. Regeneration replicates were selected to span the range of ages (2 to 19 year-old regeneration) and geographical area of the study region. The widths of streamside reserves were measured by hipchain at each transect location; distance from the stream bank to the reserve edge was measured along the ground. The 1934 wildfires were widespread in the Picton River Valley, and while it is not possible to accurately estimate *E. obliqua* stand age based on tree heights and diameters (Alcorn et al. 2001), the mature forest probably ranged in age from 1934 regrowth to >100 year-old 'old-growth', with mosaics of several fire ages common (Alcorn et al. 2001; Hickey et al. 1998). A systematic sampling design was used to collect beetles within each habitat replicate. Three transects of 6 pitfall traps each resulted in 18 traps per stand, and 360 traps in total. Transects were located 50 m apart and ≥ 100 m from roads in the case of streamside reserve treatments, and ≥ 200 m from roads or logging regeneration in the case of mature riparian and mature upslope stands. Regeneration transects were located ≥ 100 m upslope from streamside reserves, and ≥ 50 m from roads. Transects were aligned at right angles to streams, with traps located 1 m, 5 m, and 10 m either side of the stream, or either side of a 3 m wide 'imaginary stream' for regeneration and mature upslope stands. This sampling protocol was designed to collect beetles from the interior half of streamside reserves; i.e. the zone least influenced by edge effects. Riparian conditions would likely influence beetles in at least some of the zone 10 m adjacent to streams (Chapters 3 and 4).

Pitfall traps consisted of 7.5 cm diameter plastic drinking cups inserted in PVC downpipe sleeves dug into the soil. Ethylene glycol (antifreeze) was used as preservative. A plastic lid was held in place above each trap with three wooden sticks to protect traps from rainfall and disturbance. Pitfall traps were closed for at least two

Table 1. Location and stand replicate details for replicates of the four habitat types: continuous riparian forest (cs), continuous upslope forest (m), logging regeneration (r), and streamside reserve (sr). ‘FT’ refers to Forestry Tasmania. Streamside reserve widths are given for each side of the stream for each transect.

Stand	Location	FT coupe code and year of regeneration
cs1	43°10'28''S 146°39'E	between PC34F and PC35D (mature)
cs2	43°13'23''S 146°39'5"E	between PC39E and PC43D (mature)
cs3	43°10'34''S 146°41'50"E	between PC17B and PC70B (mature)
cs4	43°12'3''S 146°42'13"E	between PC70D and PC71D (mature)
cs5	43°9'50''S 146°42'24"E	between PC15C and PC17A (mature)
m1	43°10'24''S 146°39'E	PC34F (mature)
m2	43°13'21''S 146°39'9"E	PC39E (mature)
m3	43°10'29''S 146°41'52"E	PC17B (mature)
m4	43°12''S 146°42'13"E	PC70D (mature)
m5	43°9'55''S 146°42'22"E	PC17A (mature)

Stand	Location	FT coupe code and year of regeneration	Reserve widths (m)
r1	43°10'47''S 146°39'16"E	PC35G (1990)	
r2	43°11'54''S 146°39'36"E	PC38D (1983)	
r3	43°12'6''S 146°39'48"E	PC38B (1994)	
r4	43°13'27''S 146°40'6"E	PC39F (1986)	
r5	43°13'30''S 146°39'21"E	PC39D (2000)	
sr1	43°10'35''S 146°39'22"E	between PC34C (1993) and PC35G (1990)	60, 35; 60, 35; 60, 35
sr2	43°12'5''S 146°39'33"E	between PC38D(1983) and PC38B (1994)	50, 16; 50, 25; 50, 25
sr3	43°13'37''S 146°40'1"E	between PC39F (1986) and PC39D (2000)	60, 20; 60, 20; 60, 18
sr4	43°13'35''S 146°39'19"E	between PC39D (2000) and PC43A (1989)	60, 18; 60, 30; 20, 50
sr5	43°13'46''S 146°40'E	between PC39D (2000) and PC43B (1996)	40, 22; 46, 25; 50, 37

weeks before trapping to avoid digging-in effects (Greenslade 1973). Traps were operated for a four-week trapping period in spring (October – November) 2002. There were missing data for seven traps which were either flooded, or in one case, disturbed by a mammal. In no case was there more than one missing trap per stand. All beetles were removed and sorted to family and morphospecies based on external morphology and keys to family in Lawrence and Britton (1994) and Lawrence *et al.* (1999). Taxonomic knowledge of many beetle families is scarce, and identification to taxonomic species was not possible for all morphospecies. Species identifications were made by reference to the Tasmanian Forest Insect Collection at Forestry Tasmania, where the reference collection will be deposited.

Statistical Analyses

Data from the six traps within transects were pooled in analyses, which did not investigate distance effects within transects. We tested the total abundance, species richness and Margalef diversity (Magurran 2004) of beetles in transects using a nested ANOVA model where Transects (random factor) were nested within Stand (random factor) which was then nested within Habitat (continuous riparian, continuous upslope, logging regeneration, and streamside reserve), which was a fixed factor. Margalef diversity was used to assess species diversity adjusting for the total number of individuals in a sample unit, since species richness was approximately linearly related to the log of the number of individuals in our collections. We conducted planned contrasts to test for differences in diversity between streamside reserves and the three other habitat types. These tests were carried out in R Version 2.0.1 (R Development Core Team 2003).

A constrained canonical analysis of principal coordinates (CAP) ordination (Anderson 2003; Anderson & Willis 2003) and ANOSIM (Clarke & Green 1988) in

Primer v5 (Clarke & Gorley 2001) were conducted using a Bray-Curtis dissimilarity matrix from a square-root transformed dataset of the average abundance of 24 commonly collected species, based on an arbitrary abundance cut-off of 0.05% of the total number collected; 9999 permutations were used. The same nested model applied in univariate ANOVA was used for nested ANOSIM analysis while the CAP analysis used mean abundances at each stand.

Indicator species analysis (Dufrene & Legendre 1997) conducted in PC-ORD assessed the habitat preferences of individual beetle species for the four habitats. The analysis used mean abundances per stand (5 replicates) for beetle species collected more than 10 times (51 morphospecies). Indicator species analysis combines information about species' relative abundance (specificity) and relative frequency of occurrence (fidelity) in each habitat to calculate an Indicator Value (IV, %), where 0% represents no indication and 100% represents perfect indication of that habitat. A Monte Carlo *P*-value (9999 permutations) evaluates the statistical significance of the IV for each species. Reference is made to previously identified indicator species (Chapters 5 and 6) for young logging regeneration, edge-tolerant mature forest, and edge-avoiding mature forest habitats, with the caveat that species' distributions in intermediate successional ages has not been determined.

Results

The average streamside reserve width was 40 ± 6 m ($\pm 95\%$ CI) from reserve edge to stream. We collected 6,530 beetles from 226 morphospecies and 37 families; 2,472 individuals were collected of the most common morphospecies *Aleoc_1* (Staphylinidae: Aleocharinae), while just over half (52%) of morphospecies were collected only once or twice.

Nested ANOVA indicated that there were significant differences among habitats for species richness ($F_{(3,16)} = 5.918$, $P = 0.007$) and Margalef Diversity ($F_{(3,16)} = 9.462$, $P < 0.001$), but not abundance ($F_{(3,16)} = 1.016$, $P = 0.412$) of beetles. Based on planned comparisons between species richness and Margalef diversity in streamside reserves and the other three habitats, both diversity indices were similar in streamside reserves and continuous mature upslope areas but greater than in streamside reserves and continuous mature riparian areas (Fig. 1). For both indices, mean diversity was greater in logging regeneration than for streamside reserves, although this difference was only significant for Margalef diversity (Fig. 1). On average, there were approximately thirty percent more species per transect in streamside reserves than in continuous riparian areas.

Fig. 1. Number of beetle species (A), and Margalef diversity (B) in the four habitats; continuous riparian forest (cs), continuous upslope forest (m), logging regeneration (r), and streamside reserve (sr). P -values are presented for habitats found to differ significantly compared to streamside reserves in planned comparisons.

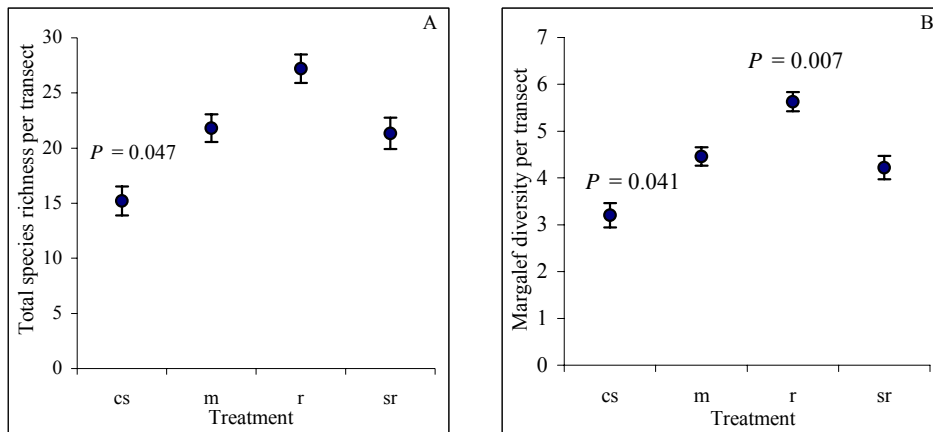
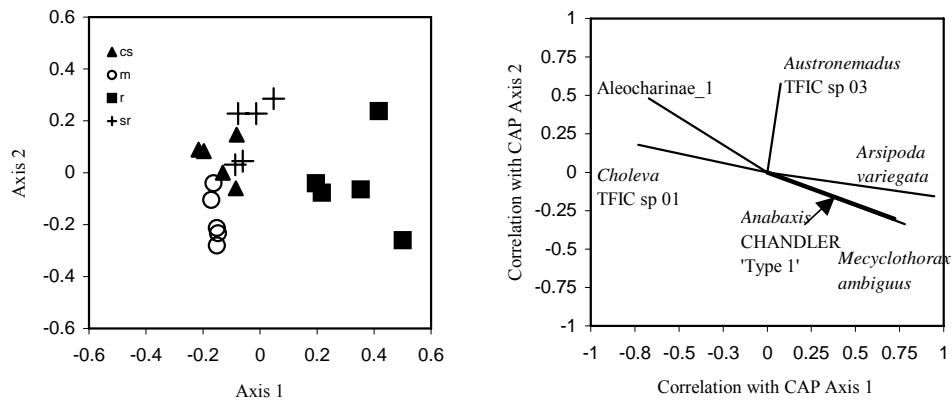


Fig. 2. Constrained CAP ordination based on common beetle assemblages in four habitats: continuous riparian (cs), continuous upslope (m), logging regeneration (r) and streamside reserves (sr). Vectors are plotted for previously identified indicator species that are correlated with the ordination with $r > |0.5|$.



The constrained CAP ordination (Fig. 2) showed a significant effect of Habitat, with a squared canonical correlation of $\delta^2 = 0.8926$ ($P < 0.001$). Young regeneration plots appeared separated from mature forest habitat plots along the horizontal axis. Positioning of mature forest plots along the vertical axis indicated a transition from continuous upslope, to continuous riparian to streamside reserve habitats. Plots from continuous riparian and upslope habitats were partially separated along the vertical axis. There was some overlap of streamside reserve and continuous riparian plots. Three of five streamside reserve plots were separated at the top of mature forest plots, while the others overlapped with the cluster of continuous riparian plots. Streamside reserve plots did not overlap in position with continuous upslope ones. Streamside reserve plots were more strongly related to mature continuous forest assemblages than to regeneration forest ones. Three of the five streamside reserve plots also clustered separately from continuous mature forest plots in an unconstrained principal coordinate analysis ordination of the same dataset (not

presented), corroborating patterns illustrated in Fig. 2. Leave-one-out allocations successfully classified 53% of continuous riparian, 67% of continuous upslope, 80% of streamside reserve and 87% of logging regeneration observations.

The three beetle species associated with regeneration plots in Fig. 2 were indicators of young logging regeneration (Chapter 5). The mature forest edge-avoiding indicator *Choleva* TFIC sp 01 (Leiodidae) was associated with continuous mature (mostly riparian) plots, while the mature forest indicator *Aleoc*_1 (Staphylinidae) was associated with an overlapping area of continuous riparian and streamside reserve plots (Fig. 2). *Austronemadus* TFIC sp 03 (Leiodidae) was associated with streamside reserve plots, and is also an indicator of mature forest (Chapter 5).

Nested ANOSIM indicated significant assemblage differences among habitats (Global $R = 0.345$, $P < 0.001$). Post-hoc comparisons found young regeneration differed significantly from the other three habitats ($P < 0.001$), and that streamside reserve assemblages differed significantly from both continuous riparian ($R = 0.192$, $P = 0.048$) and continuous upslope assemblages ($R = 0.196$, $P = 0.048$), but did not detect differences between continuous upslope and continuous riparian habitats ($R = 0.016$, $P = 0.413$).

The indicator species analysis (Table 2) further revealed species patterning in streamside reserves compared to the other three habitats. The Indicator Value of young forest indicator species was $\leq 2\%$ in streamside reserves, suggesting that habitat in the interior of these reserves was unsuitable for species specialized to young forest. Edge-avoiding indicators of mature forest were of generally lower Indicator Value (%IV) in streamside reserves than continuous upslope areas.

Decilaus lateralis (Curculionidae) had lower %IV in streamside reserves (3%) than in continuous riparian areas (27%), while the other three edge-avoiding species were also of relatively low %IV in continuous riparian areas. By contrast, edge-tolerant indicators of mature forest in all cases showed greatest Indicator Value in the streamside reserves. These results suggest that the interior habitat of streamside reserves supports beetle species with habitat affinities for mature, but not regeneration, forest. However habitat suitability for edge-avoiding mature forest species appears to be compromised relative to continuous upslope mature forest areas.

Habitat affinities were also found for eight commonly collected species for which we did not have prior knowledge about habitat preferences (Table 2). *Stichonotus leai* (Carabidae) and *Decilaus* TFIC sp 04 (Curculionidae) had smaller Indicator Values in streamside reserves and continuous riparian areas than in continuous upslope mature forest. These species were too rare to be included in the datasets previously used to identify edge-avoidance or other habitat preferences (Chapters 5 and 6), but they are possibly also edge-avoiding, mature forest specialists. Six beetle species, *Eupines* CHANDLER ‘Tasmania 1’, *Euplec*_6, *Aleoc*_10, *Anotylus* TFIC sp 03 and 04 (all Staphylinidae), and *Aspidiphorus humeralis* (Sphindidae), were not common enough to be included in analyses in Chapter 5, but based on the results of the present study (which included older logging regeneration), are probably also specialized for conditions in regenerating forest. Unlike the other regeneration preferring species, *Aspidiphorus humeralis* was also of intermediate Indicator Value in streamside reserves.

Table 2. Indicator Value (%) for beetle species in continuous riparian (cs), continuous upslope (m), young logging regeneration (r) and streamside reserves (sr). Species presented were either previously identified as significant indicators of mature interior habitat (Chapter 6), mature forest (Chapter 5), or regeneration forest (Chapter 5), or were significant in this analysis. Species with permutation test P -value <0.05 are indicators of forest habitat type.

Species	Indicator Value				P-value
	cs	m	r	sr	
<i>Indicators of mature forest, edge-avoiding</i>					
Leiodidae: Cholevinae: <i>Choleva</i> TFIC sp 01	19	43	2	34	0.048
Curculionidae: Cryptorhynchinae: <i>Decilaus nigronotatus</i> Lea, 1913	15	43	1	14	0.149
Curculionidae: Cryptorhynchinae: <i>Decilaus striatus</i> Lea, 1913	8	62	0	7	0.009
Curculionidae: Cryptorhynchinae: <i>Decilaus lateralis</i> Lea, 1913	27	17	0	3	0.376
Average IV's	17.3	41.3	0.8	14.5	
<i>Indicators of mature forest, edge-tolerant</i>					
Leiodidae: Cholevinae: <i>Austronemadus</i> TFIC sp 03	17	13	25	38	0.232
Staphylinidae: Aleocharinae: <i>Aleoc</i> _1	31	23	7	39	0.048
Staphylinidae: Aleocharinae: TFIC sp 02	15	16	12	53	0.043
Melandryidae: Melandryinae: <i>Orchesia alphabetica</i> Lea	30	4	3	32	0.382
Average IV's	23.3	14.0	11.8	40.5	

Species	Indicator Value				P-value
	cs	m	r	sr	
Carabidae: Psydrinae: <i>Mecyclothorax ambiguus</i> (Erichson, 1842)	0	0	80	0	0.004
Leiodidae: Leiodinae: <i>Zeadolopus</i> sp3	2	0	67	2	0.009
Staphylinidae: Pselaphinae: <i>Anabaxis</i> CHANDLER 'Type 1'	0	0	79	0	0.005
Chrysomelidae: Galerucinae: <i>Arsipoda variegata</i> (Westwood, 1838)	0	0	100	0	<0.001
Average IV's	0.8	0.0	82.4	0.6	
<i>Other species</i>					
Carabidae: Carabinae: <i>Stichonotus leai</i> Sloane, 1910	1	64	0	6	0.011
Staphylinidae: Pselaphinae: <i>Eupines</i> CHANDLER 'Tasmania 1'	0	0	60	0	0.035
Staphylinidae: Pselaphinae: <i>Euplec6</i>	1	3	79	7	0.004
Staphylinidae: Aleocharinae: <i>Aleoc_10</i>	1	2	79	1	0.003
Staphylinidae: Oxytelinae: <i>Anotylus</i> TFIC sp 04	0	0	76	1	0.006
Staphylinidae: Oxytelinae: <i>Anotylus</i> TFIC sp 03	0	0	78	1	0.003
Sphindidae: <i>Aspidiphorus humeralis</i> Blackburn, 1894	0	0	57	24	0.018
Curculionidae: Cryptorhynchinae: <i>Decilaus</i> TFIC sp 04	5	68	0	7	0.003
Average IV's	1.0	17.1	53.6	5.9	

Discussion

Beetle assemblages in streamside reserves mostly reflected our predictions:

1. Streamside reserve beetle assemblages differed from the other three habitats (i.e. from riparian and upslope areas in continuous forest, and logging regeneration). This suggests that streamside reserves do not provide equivalent habitat for beetles to continuous forest areas.
2. Assemblage composition in streamside reserves was much more representative of a mature forest than a regeneration forest beetle community, supporting very low abundances of beetle species with known preferences for young regeneration. This implies that the habitat value of streamside reserves is more equivalent to continuous mature forest than to logging regeneration forest.
3. The species richness and Margalef diversity of beetles were significantly greater in streamside reserves than in continuous mature riparian areas, a result that appeared to be largely caused by disturbance-related changes to species interactions for mature forest specialists and species inhabiting both mature and regeneration habitats, but also related to a few additional regeneration-characteristic species infiltrating into streamside reserves.
4. Edge-avoiding mature forest species had lower Indicator Values in streamside reserves than did edge-tolerant mature forest species, suggesting that streamside reserves may not provide adequate habitat for edge-sensitive species. The Indicator Values of three of the four known edge-avoiding species were also relatively low in continuous forest riparian areas, although the explanation for this was unclear.

Streamside reserve beetle assemblages were most similar to those in continuous riparian areas. Greater similarity to continuous riparian than upslope

assemblages is not surprising, since we sampled the riparian areas towards the interior of the streamside reserves. However, species diversity in streamside reserves was elevated relative to continuous riparian areas, up to a level equivalent with continuous upslope areas. Since abundance did not differ among habitats, the increased richness appears to arise from the addition of species (see below) together with decreases in the abundance of some species, rather than from species packing caused by beetles moving towards the reserve interior (Saunders et al. 1991). Edge effects throughout the streamside reserves are probably responsible for these changes to diversity and assemblage composition. Increased richness of beetles is commonly observed in edge-affected areas, and is often associated with an influx of species from the adjoining habitat (Davies et al. 2001; Didham 1997; Driscoll & Weir 2005; Halme & Niemelä 1993). Species preferring young forest were of low Indicator Value in streamside reserves, except for one species with an apparent preference for young forest, *Aspidiphorus humeralis* (Sphindidae), that also had moderate Indicator Values in streamside reserves. Occasional movement into reserves by young forest species could, however, inflate diversity measures in this habitat. Disturbance by edge effects may create conditions suitable for some rarer mature forest species, thus inflating beetle diversity in streamside reserves.

In the present study, edge-tolerant mature forest affiliated species had higher Indicator Values in streamside reserves than in the other three habitats, and *Austronemadus* TFIC sp 03 (Leiodidae) was also associated with streamside reserve plots in the ordination. Some studies have identified species that are affiliated with edge-affected habitats (e.g. Driscoll & Weir 2005; Magura & Tóthmérész 1997), although none were identified from the previous edge effects study conducted in this forest type (Chapter 6). Greater Indicator Values of edge-tolerant species in streamside reserves in this study could relate to the additional influence of area

effects (sensu Didham et al. 1998) where streamside reserves had been logged on both sides, although no information currently exists about the area-sensitivity of Tasmanian beetles. In contrast to edge-tolerant species, edge-avoiding mature forest species had smaller Indicator Values in streamside reserves than in continuous upslope areas, as did *Decilaus* TFIC sp 04 (Curculionidae) and *Stichonotus leai* (Carabidae). Most of these species also had small Indicator Values in continuous riparian areas in this study. However, in a previous study, none of these species were identified as significant indicators of upslope habitat, and their Indicator Values were not consistently lower in riparian than upslope areas (Appendix 3). The previous riparian study did find that common species, overall, were less abundant in riparian areas (Chapter 4). Perhaps these edge-sensitive species are less common in areas of rapid ecological transition, and thus were of less abundant in riparian than upslope areas in this study, although logging coupe edges have also previously been demonstrated to support different beetle assemblages to riparian areas (Chapter 7). Because our study design sampled the riparian area towards the interior of the streamside reserves, we cannot rule out the possibility that these species might be more common further upslope in the streamside reserves. However, based on their known edge-sensitivity, and the prediction that reserves of this width would be entirely edge-affected, this seems unlikely.

Our findings are similar to those of Mönkkönen and Mutanen (2003), and suggest that beetle species that benefit most from streamside reserves are probably mature forest specialists that are insensitive to edge conditions. It is unfortunate then, if sensitive edge-avoiding species are disadvantaged in reserve corridors, as such species are more likely to suffer negative consequences of current logging practices, and potentially benefit most from effective corridors for habitat and dispersal (Hill 1995; Rosenberg et al. 1997). Although the particular edge-sensitive indicator

species referred to here are potentially common and widespread enough to be effectively conserved by existing large formal reserves, the likely fate of the rarer majority of beetle species is very difficult to assess. Davies et al. (2004) found that a synergistic effect placed beetle species that were both rare and specialized at particular risk of local extinction, suggesting that reserves in logging areas that effectively conserve edge-sensitive species are essential.

While streamside reserves in Tasmania have as their primary objective the protection of aquatic values rather than the conservation of terrestrial species, wildlife habitat strips are intended primarily for conservation. The widths of the streamside reserves assessed in this study were intermediate between the minimum widths prescribed for streamside buffers, and the 100 m total minimum width prescribed for wildlife habitat strips (Forest Practices Board 2000). Reserve corridors containing core habitat not subject to edge influences are recommended for conservation of edge-avoiding mature forest specialists (Hobbs 1992; Soulé & Gilpin 1991). Since edge effects into streamside reserves probably penetrate at least as far as 65 m (Chapter 7), riparian corridors would probably need to exceed 130 m width to contain any core habitat. Wider reserves still may be needed if the objective were to maintain species that are sensitive to both edge and area effects (Didham et al. 1998; Laurance et al. 2002). Implementing wider riparian corridors, e.g. 200 m wide wildlife habitat strips, and monitoring their effectiveness for habitat and dispersal of various taxa, could be employed as part of an adaptive management framework (Lindenmayer & Franklin 2002).

This study was limited to assessing habitat suitability of streamside reserves for ground-dwelling beetles in the first 20 years following harvesting. Future research could investigate longer-term outcomes over the approximately 90 year harvesting rotations. Based on other studies, it is possible, although not certain, that

edge effects may dissipate with time (Kapos et al. 1997; Matlack 1994; Ries et al. 2004), and that habitat value of streamside reserves could improve as the adjacent regeneration ages. Forest either side of the reserves in this study were in all cases harvested within 14 years of each other. Whether greater separation in time of the harvesting of adjacent coupes could enhance reserve integrity also warrants investigation. On the other hand, the long-term integrity of reserve corridors could be compromised because of edge creep associated with elevated levels of windthrow of trees near the reserve edges (Kapos et al. 1997; Westphalen 2003), a phenomenon that could be particularly insidious over several rotations. Corridors are prone to a relatively high influence of edge effects compared to approximately circular-shaped reserves of equivalent area; however, corridors potentially have benefits for facilitating landscape connectivity and dispersal (Laurance & Yensen 1991; Rosenberg et al. 1997). Therefore, it may be worth considering including a mix of these approaches in the overall production forest reservation strategy.

Our study did not differentiate between the functions of streamside reserves for habitat versus dispersal of beetles. Reserve corridors have the potential to fulfill both these roles (Mönkkönen & Mutanen 2003; Niemelä 2001), especially for species such as many ground-dwelling invertebrates that have localized areas of occupancy by individuals, and low dispersal abilities. The ability of mature forest specialists to disperse across young regeneration, and the role of corridors in facilitating dispersal between stands of intact mature forest needs investigation to assess the relative merits of corridors compared to other reserve-allocation strategies. Some of the mature forest specialists were collected extremely infrequently in young regeneration (this study, Chapter 5), and may not disperse through young habitat. Such information would be essential to inform crucial decisions about whether it is better to allocate reserves as corridors (wildlife habitat strips), to facilitate dispersal,

or as patches, to minimize edge and area effects (Mönkkönen & Mutanen 2003; Rosenberg et al. 1997; Saunders & Hobbs 1991).

Conclusion

Streamside reserves have a role in providing habitat for edge-tolerant mature forest beetle species. However, edge effects over the entire width of streamside reserves appear to compromise their habitat suitability for edge-avoiding beetle species. Since edge-avoiding species are likely to be amongst the most sensitive to forest management practices, ensuring that there are enough reserves in the landscape of sufficient size to contain interior habitat is important if biodiversity conservation goals are to be met. While recognizing that streamside reserves are primarily intended to protect aquatic values, if their areas are to be included in estimates of mature forest in the terrestrial reserve system, the fact that their relatively narrow widths appear to reduce their habitat value for some edge-avoiding ground-dwelling beetle species should be acknowledged. Ensuring wildlife habitat strips contain interior habitat would realize their intended role for maintaining habitat for biodiversity. In Tasmania, where intensive forest management is relatively recent, we have the opportunity of ensuring that reserves and retained corridors are wide enough to provide effective habitat for even sensitive species. Wider reserves are recommended to effectively conserve species that avoid edge-affected habitat.

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Chapter 9

General Discussion

An overview of factors influencing ground-dwelling beetle distributions in production wet eucalypt forest and their relevance to reserve design

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Abstract

Conservation of biodiversity is an important goal of contemporary sustainable native forest management. Ground-dwelling beetles are sensitive to forest management practices and fragmentation, yet the taxonomic impediment and limited species-specific information about their ecology has meant that habitat requirements of beetles and other invertebrates are rarely considered explicitly in management planning. Studies of ground-dwelling beetles in wet eucalypt forest investigated distributions in relation to forest age, spatial separation, and riparian and edge gradients. Successional age (young versus mature forest) was the strongest determinant of beetle assemblage composition, followed by site-to-site turnover within the 18 x 18 km main study area. Riparian and edge effects on beetles were weaker in their overall influence, although important in different ways. Findings that fewer beetles occur near streams than upslope, and that some beetles are edge avoiding mature forest dependent species, are relevant to conservation planning and reserve design. An interaction between edge and riparian effects appeared to be responsible for a greater depth of edge penetration into riparian than upslope habitat. Results of these studies suggest that wildlife habitat strips need to be wider, and more frequently positioned upslope, if they are to provide habitat for ground-dwelling beetles of comparable quality to continuous unlogged habitat. Suggestions are provided for worthwhile topics for further research.

Introduction

Wet eucalypt forest in Tasmania, Australia, is important both ecologically and socio-economically, and finding a balance between conservation of biodiversity and wood production is challenging. Heated debate amongst those supporting and opposing native forest logging has created a politically charged climate. Research aimed at better understanding the ecology of the forest, and the impacts of forest management practices, can contribute greatly towards ensuring that where native forest harvesting is practiced, it is done in an ecologically sustainable manner. Lack of knowledge of the ecology and requirements of forest biota, including beetles, has been a serious impediment to the development of silvicultural practices that ensure metapopulation persistence in timber production areas. Reserve corridors (streamside reserves and wildlife habitat strips, Forest Practices Board, 2000) in logging areas have the potential to contribute greatly in this regard, assuming their widths and positioning are adequate to meet the diverse needs of the large number of ground-dwelling beetle species. The studies presented in this thesis increase our understanding of the ecological distributions of ground-dwelling beetles in wet eucalypt forest.

Knowledge about the response of beetles to forest age, site separation, riparian gradients and edge effects from logging coupes are relevant to designing reserve corridor networks that will make a significant contribution towards their conservation. This chapter summarises the foregoing findings, discusses them in the context of current and potential reservation strategies, and highlights worthwhile research areas for future studies. The ecological patterning of the beetles are situated in the context of current management practices in wet eucalypt forests, and recent thinking about the relative merits of different management strategies for landscapes subject to fragmentation and relatively short harvesting rotations.

Ecological patterning of ground-dwelling beetles in wet eucalypt forest

The response of beetles to a variety of factors will influence their distributions and sensitivity to forest management practices at both site and landscape scales. This thesis, and some other Tasmanian beetle studies, have documented beetle distributions in relation to forest successional age, spatial separation at local (within 100 m) and regional scales, riparian influences, edge effects (into both non-riparian and riparian habitat), and in streamside reserves compared to continuous forest. These patterns in beetle distributions are summarised here.

Response of beetles to successional age

The species composition of ground-dwelling beetles differed substantially between logging regeneration and unlogged mature *Eucalyptus obliqua* dominated forest (Chapters 5 and 8). An indicator species analysis (Dufrêne and Legendre, 1997, Chapter 5) identified several species characteristic of ≤ 5 -year-old regeneration and mature undisturbed forest (Table 1). These indicator species were found to be robust indicators of logging regeneration and mature unlogged forest in a second study conducted at separate sites (Chapter 8). The second study also identified additional indicator species that appear to be representative of both < 20 -year-old logging regeneration and mature unlogged forest successional stages (Table 1). In Chapter 5, 43% of commonly collected species met the criteria to be classified as indicator species for forest age. Approximately equal numbers of mature (7 species) and young (9 species) characteristic species were identified, but based on their Indicator Values, the young forest indicators appeared to be slightly more strongly restricted to young regeneration habitat. Of the 21 species not identified to be significant indicators of

successional age, all but three were collected more than twice as often in one age class or other, thus appearing to have successional age preferences without being confined to that habitat. Only one commonly collected species, *Baeocera* TFIC sp. 02 (Staphylinidae) was considered to be a true generalist for both young and mature forest (Chapter 5). Additional regeneration forest indicators were identified in the second study (Table 1), possibly because of the inclusion of older regeneration in this study. Since the studies did not assess the distributions of beetle species in older regeneration forest, the indicator species should only be referred to in the context of comparisons between mature unlogged forest and young logging regeneration.

The overall abundance and species richness responses of beetles to forest age differed somewhat between the two field studies. In the first study, abundance was significantly greater in ≤ 5 -year-old regeneration than in mature unlogged forest, but species richness was greater only at Picton (Chapter 5). In the second study, abundance did not differ between < 20 -year old regeneration and mature forest, but species richness was greater in the regeneration (Chapter 8). It is unclear why the regeneration forest has more individuals in one study and more species in the other, especially since abundance and species richness are usually related (Magurran, 2004). However, higher species richness in young regeneration than in mature forest is also typical of boreal forests (Niemelä, 2001).

Based on the degree of scatter in ordination plots, there appeared to be more variation in beetle assemblage composition in regeneration than mature forest (Chapters 5 and 8), possibly because species composition shifts rapidly in response to habitat differences across the range of regeneration ages.

Since modern silvicultural practices have only been applied in this forest type since the 1960s, refining our understanding of longer-term successional transitions in species composition following logging will need to be an ongoing process. The shift

from natural wildfire disturbance to logging as the dominant regeneration process raises the question of whether all young forest specialist species will persist in the absence of natural wildfires (Baker et al., 2004; Buddle et al., 2006). The age-class distribution and relative scales of patchiness of naturally wildfire regenerated forest could guide timber management planning (Hickey et al., 1998; Marsden Smedley, 1998; Baker et al., 2004). Wet forest successional processes should continue to be a relevant area of research within the scope of the Warra LTER, which is a focal point for long-term ecological research within the wet eucalypt forest ecosystem (Brown et al., 2001). Understanding habitat use by beetles in intermediate successional stages (e.g. Michaels, 1999) is important, since the impacts of fragmentation on beetles will depend on the degree to which particular species are able to disperse through the matrix (Ås, 1993; Davies et al., 2004; Driscoll, 2005). In a previous study in the same area, Michaels found wet forest ground-dwelling beetles with preferences for young, intermediate and older successional stages (Michaels and McQuillan, 1995; Michaels, 1999; Michaels and Bornemissza, 1999). For species identified in this thesis as having a preference for mature over young forest, the regeneration matrix is likely to become more inhabitable as the regeneration ages. For example, Michaels and McQuillan (1995) considered the carabid *Chylmus ater* to be an old-growth specialist species based on a chronosequence study assessing logging regeneration up to 24 years since harvesting, but this species was the third most common carabid collected in a study in 33-year old clearfelling regeneration (Baker, 2000). Most of the mature forest indicators in these studies have been collected occasionally in intermediate-aged regeneration in other studies (Baker et al., 2004; Yee, 2005), while the staphylinid *Aleoc_1* was commonly collected in 33-year-old regeneration and the saproxylic weevil *Decilaus lateralis* was common in samples from logs in 20-30-year-old logging regeneration (Yee, 2005). Further investigation of the age at which

forest becomes suitable habitat for species identified as mature forest indicators in this thesis would be useful.

Many of the beetle species collected in these pitfall-trapping studies were also collected in a contemporary study of the log fauna in the same area (Yee, 2005).

Many of these species are dependent on rotting logs for larval habitat (Yee, 2005) but inhabit the leaf litter as adults. Yee (2005) compared beetle assemblages in large and small *E. obliqua* logs, and found several species that were indicators of large logs and their associated fungal decay communities. Since large logs will originate from old-growth forests but not from clearfelling regeneration on 90-year rotations, Yee's study demonstrates that there are specific habitat features (logs) related to forest age and harvesting history that control the beetle assemblages in these forests. Hopkins et al. (2005) also found greater species richness of saproxylic beetles in living >150-year-old Tasmanian *E. obliqua* than in younger age classes, while Bar-Ness (2005) found some differences in assemblage composition between beetles in old-growth *E. obliqua* canopies compared to approximately 100-year old trees in the same region.

In south-west Tasmania, Driscoll (2005) found relatively little difference between the beetle assemblages in mature eucalypt forest and rainforest (a later successional stage, Jackson, 1968), although both forest types had very different beetle assemblages to nearby buttongrass. Not surprisingly, beetle species composition was also found to differ substantially between damp sclerophyll forest in northern Tasmania and young plantations of *Pinus radiata* and *E. globulus* (Grove and Yaxley, 2005). The degree to which plantations are comparable to young successional native forest has not been investigated, but they are likely to be more similar to young than to mature native forest. Based on these studies, Tasmanian beetles appear to be highly sensitive to forest successional age, and to habitat

Field Code Changed

features (tree and log age) associated with current or previous forest age. Therefore, forest age can be considered to be an important determinant of beetle distributions.

Sensitivity to forest age means that beetles are likely to be sensitive to various aspects of forest management. The indicator species identified in Chapter 5 proved useful in detecting and describing edge effects (Chapter 6 and 7), illustrating the relevance of elucidating general habitat preferences as background information to improve the ability to detect more complex ecological patterning. The loss of old-growth habitat under silvicultural systems employing successive ~90-year rotations is an important concern in the light of a review by Fahrig (2003) which indicated that habitat loss has consistently large negative consequences on biodiversity, while the effects of fragmentation *per se* (i.e. the breaking apart of habitat) are much weaker, and as likely to be positive as negative.

Response of beetles to spatial separation

In the 18 x 18 km area encompassed by the main part of this study, the turnover of beetle assemblages among sites was evident in both regeneration (Chapter 5) and mature forest (Chapters 2 and 5) habitats. It is interesting to explore the relative influence on beetle distributions of turnover among sites compared to other ecological influences. Of the factors affecting ground-dwelling beetle distributions explored in this thesis, successional age (young regeneration versus mature unlogged forest) was the only effect that outweighed the influence of site turnover on beetle assemblages (Chapter 5). Site turnover was a stronger overall influence on assemblage composition than either riparian (Chapter 3) or edge effects (Chapter 6). Site turnover affected assemblage composition, species richness and abundance of beetles (Chapters 2-7). Overall, the Kermandie area had the greatest abundance and richness of beetles, and more distinct assemblage composition (Chapters 2, 4, 5).

Variance components analysis of beetle data from Baker (2000) for all coleopterans and commonly occurring taxa alone found that ~10-40% of variation in abundance and species richness was accounted for at the site level, with variation amongst individual pitfall traps accounting for the majority (~50-85%) of variation (Appendix 2). High local-scale patchiness over as little as a few metres, illustrated in Chapter 2, is common for ground-dwelling beetles (e.g. Niemelä et al., 1992; Niemelä et al., 1996). However spatial variation within the scale of 99 m sampling transects did not appear to cause patterning in beetle abundance, species richness or assemblage composition (Chapter 2). It was important to be able to rule out the potential influences of pitfall trap depletion or spatial autocorrelation, related to the primary transect design with pitfall traps placed at unequal distances, in the other studies described in this thesis. These influences should also be considered in similar studies in other ecosystems.

The importance of beetle assemblage turnover amongst study sites has been highlighted in several other Tasmanian beetle studies (Baker et al., 2004; Grove and Yaxley, 2005; Yee, 2005). Restricted distributions have been recorded for several beetle species (Bryant and Jackson, 1999). Rapid assemblage turnover for ground-dwelling and saproxylic beetles is probably relevant in Tasmanian forests generally, and has implications for the design and interpretation of ecological studies of beetles in the region. It highlights the importance of spatial influences on beetles, and that studies should not confound treatments with geographical separation. Exploration of spatial scales important to biological organisation (e.g. Niemelä, 1990; Niemelä and Spence, 1994) is an important area of research, and one that needs to be extended to regional scales in studies of beetle distributions in Tasmanian forest.

Presently, the specific factors responsible for species distributions are poorly understood, and many interacting factors are probably at play, e.g. vegetation, habitat

structure, fire history, nutrient status, aspect, elevation (Michaels and McQuillan, 1995; Baker, 2000). Recent research in the field of ecological genetics suggests that foundation tree species can have an ‘extended phenotype’ that affects the much broader ecological community (Whitham et al., 2003). For example, within-species genetic variation in plantation *Eucalyptus globulus* (Baker and Barbour, unpublished data) has been shown to affect the ground-dwelling invertebrate community. Litter decomposition (Schweitzer et al. 2005a, 2005b) and microbial community composition (Schweitzer, pers. comm.) have been found to differ with tree genotype in native *Populus* forest at both individual tree and landscape scales. Whether the scale of genetic variation in *E. obliqua* has flow-on impacts that could partially explain site-to-site turnover in ground-dwelling beetle assemblages could provide an interesting topic for further research. The relevance of assemblage turnover to reservation strategies is discussed below.

Response of beetles to riparian influences

Assemblages of ground-dwelling beetle were found to respond to riparian influences at the edges of small streams. Beetle abundance, species richness and assemblage composition changed in response to the riparian-upslope gradients (Chapters 3 and 4). Like the response of beetles to successional age, their abundance and species richness in riparian compared to upslope areas in unlogged continuous forest differed between the two research studies. In the first study, beetles were found to be less abundant near streams than upslope, but they were less speciose than upslope only near King Creek at Warra (Chapter 4). In contrast, the second study did not detect reduced abundance in riparian compared to upslope areas, but species richness was lower in riparian zones (Chapter 8). As for the successional age comparisons discussed above, the reason for different riparian responses between the two studies

is unclear, but the general pattern appears to be for reduced abundance and/or species richness of beetles near streams. These were unexpected results, since riparian areas are often considered to support relatively high total abundance and number of species of animals (Gregory et al., 1991; Catterall, 1993; Pollock, 1998; Naiman et al., 2000), and this had been found to be the case in other studies of beetles in areas where annual rainfall also exceeds 1000 mm (Brenner, 2000; Catterall et al., 2001; Davis et al., 2001; Hutchens and Wallace, 2002). Unlike riparian areas in most ecosystems, small streams in Tasmanian wet eucalypt forest do not generally have distinct riparian vegetation strips, suggesting that moisture levels upslope are not limiting. Neither of the studies reported here detected riparian or upslope indicator species (Chapters 3, 4, 8 and Appendix 3), although in the second study the trend was for lower Indicator Value of edge-sensitive species in riparian than upslope habitat in continuous mature forest. Riparian zone width was found to vary among streams from approximately 5 m to 100 m (Chapters 3 and 4), probably in relation to site characteristics such as topography and stream size. Of the factors examined in this thesis for their affect on beetle distributions, riparian influences appeared to be the subtlest.

Response of beetles to edge effects

The high level of sensitivity of beetles to habitat differences between young logging regeneration and mature unlogged forest suggested the potential for edge effects at the transition between these habitats. Ground-dwelling beetles have been found to be sensitive to edge effects elsewhere (Didham, 1997; Magura and Tóthmérész, 1997; Davies and Margules, 1998; Peltonen and Heliövaara, 1998; Grove and Yaxley, 2005), including at the edges of clearfelled logging coupes (Helle and Muona, 1985; Spence et al., 1996). This study differentiated between coupe edges adjacent to

upslope habitat (Chapter 6) and those bordering streamside reserves (Chapter 7). Other studies have found the expression of edge effects to differ with various site characteristics such as edge aspect and the degree of contrast between adjacent habitats (Ries et al., 2004), although differences between riparian and upslope edges have rarely been considered. However, both these edge types are common in wet forest logging coupes, suggesting that interaction with riparian influences on beetles could cause differing edge responses at riparian compared to non-riparian habitats. Beetles responded to edge effects at clearfelled logging coupes, and edge influence was estimated to extend further (up to approximately 65 m, Chapter 7) into streamside reserve than into upslope (~22 m, Chapter 6) habitat. Penetration of edge effects did not vary among the four non-riparian edges studied (Chapter 6), while effects differed among the four streamside reserve edges (Chapter 7). Disruption of riparian-upslope gradients is a potential explanation for the deeper penetration into streamside reserve edges. Varying streamside reserve widths, as well as possible differences in the strength of riparian effects, were likely explanations for variation among the four streams (Chapter 7). Further research to confirm these hypotheses would be worthwhile, since these studies were limited to four coupe edges of each habitat, which were not matched for aspect.

An indicator species analysis (Chapter 6) identified four edge-avoiding beetle species characteristic of mature forest interior (Table 1). At least 50% of commonly collected mature forest species were also sensitive to edges (Chapters 6 and 8), and presumably an equivalent proportion of the more rarely collected beetle species are also likely to be edge-avoiding. No beetle species appeared to have strong affinities for the edge-affected area (Chapter 6), and some other studies of beetles have also failed to detect edge-affiliated species (e.g. Spence et al., 1996; Heliölä et al., 2001). These studies (Chapters 6 and 7), and beetle community responses in the Wog Wog

fragmentation experiment in New South Wales (Davies et al., 2001), illustrate that the potential for differing responses in riparian and upslope habitats should be considered in fragmentation and edge effects research. The finding of deeper edge penetration into riparian compared to non-riparian habitat has important conservation implications (discussed below), and explicitly considering fragmentation impacts in riparian as well as upslope habitat would be relevant in other ecosystems, and worldwide. Only one other Tasmanian study has assessed edge effects on beetles in Tasmania (Grove and Yaxley, 2005). Their study suggested that edge effects from logging roads into upslope damp sclerophyll forest varied amongst study sites, possibly penetrating 100-200m. The demonstration that beetles responded to edge effects, and that some species are edge-avoiding, is evidence that fragmentation *per se* (as distinguished from habitat loss, Fahrig, 2003) of mature forest habitat is having negative consequences for ground-dwelling beetles in this ecosystem.

Beetles in streamside reserves compared to continuous unlogged forest

Based on the penetration of edge effects into streamside reserves that had been logged on only one side (Chapter 7), it was predicted that the ground-dwelling beetle assemblages in streamside reserves with logging regeneration either side would be entirely edge effected. The second study verified this prediction (Chapter 8); ground-dwelling beetle assemblages towards the interior of streamside reserves differed in assemblage composition to those in both riparian and upslope habitats in continuous forest. Streamside reserves provided habitat for mature forest beetle assemblages, however edge-avoiding species appeared to be disadvantaged. Edge-tolerant, mature forest beetle species were of greatest indicator value in streamside reserves (Chapter 8), appearing well adapted to conditions in edge-affected, and possibly area-affected, forest. Three other Tasmanian studies have assessed ground-dwelling beetle

assemblages in reserve corridors (riparian and non-riparian) compared to continuous forest, with mixed results (Taylor et al., 2000; Grove, 2004; Grove and Yaxley, 2005). One hundred meter wide non-riparian wildlife habitat strips in north-east (Grove and Yaxley, 2005) and central (Grove, 2004) Tasmania provided habitat for mature native forest beetle species, although species composition in habitat strips differed somewhat from continuous unlogged forest. Results from Taylor et al.'s (2000) study of carabids in streamside reserves in wet forest were ambiguous. The present studies illustrate how understanding habitat preferences of individual species for different successional ages (Chapter 5) and sensitivity of these species to edge effects (Chapter 6) can help assess the habitat value of reserves such as streamside reserves (Chapter 8).

Reservation strategies for beetle conservation

The studies in this thesis suggest that conservation efforts are required to ensure the persistence of populations of ground-dwelling beetle species in production forests. Several lines of evidence support this contention:

- ground-dwelling beetles were subject to edge effects, providing evidence that fragmentation has impacts on beetles, and suggesting that reserve corridors will be partially or entirely edge-affected;
- mature forest characteristic species were identified, some of which were edge-avoiders, suggesting old-growth habitat loss and fragmentation will have negative impacts for some species;
- the high level of variation in assemblage composition among sites illustrates the need for reservation across the landscape;

- differing species composition, lower beetle abundance and/or species richness, combined with deeper penetration of edge effects into riparian than upslope areas, suggest that concentration of reserve corridors in riparian areas is probably not the best conservation strategy.

Further support for these conclusions was provided by the second study which found that existing streamside reserves with clearfelled logging regeneration on either side were not of comparable habitat value to continuous unlogged mature forests, with edge-avoiding beetle species appearing to be most disadvantaged.

Beetle community composition varied significantly at the scale of several kilometres, even within relatively uniform habitat. The significance of spatial turnover to conservation management is therefore important; reservation across the managed forest landscape is needed to adequately conserve beetle fauna, since one or few reserves will probably not be representative of forest communities within the management district. Hence habitat strips, if wide enough to provide habitat in their own right, could contribute greatly to biodiversity conservation by crossing the forest landscape and improving the spatial representation of areas that are protected. Future research aimed specifically at determining what spatial scales are most important for influencing species composition and persistence (e.g. Summerville et al., 2003) would be beneficial, although processes operating over a range of scales are probably important (Niemelä and Spence, 1994; Summerville et al., 2003).

The general riparian response (fewer overall individuals and/or species of beetles near to streams) suggests that the riparian zone may be sub-optimal habitat for ground-dwelling beetles. This is of concern, given the current practice of aligning the majority of wildlife habitat strips in riparian areas. In combination with the network of streamside reserves, the result is a predominantly riparian-aligned reserve corridor network (Forest Practices Board, 2000).

Table 1. Ground-dwelling beetle species that are indicators of forest habitat type. The thesis chapter number indicates where species' habitat preferences were identified. Species denoted with a question mark are presumed to be indicators, but require confirmation.

Species	Thesis chapter
Generalist	
Staphylinidae: Scaphidiinae: <i>Baeocera</i> TFIC sp 02	? 5
Mature forest, edge-tolerant	
Leiodidae: Cholevinae: <i>Austronemadus</i> TFIC sp 03	5, 6
Staphylinidae: Aleocharinae: <i>Atheta</i> sp. (Aleoc_1)	5, 6
Staphylinidae: Aleocharinae: TFIC sp 02	5, 6
Melandryidae: Melandryinae: <i>Orchesia alphabetica</i> Lea	5, 6
Mature forest, edge-avoiding	
Carabidae: Carabinae: <i>Stichonotus leai</i> Sloane, 1910	? 8
Leiodidae: Cholevinae: <i>Choleva</i> TFIC sp 01	5, 6
Curculionidae: Cryptorhynchinae: <i>Decilaus nigronotatus</i> Lea, 1913	5, 6
Curculionidae: Cryptorhynchinae: <i>Decilaus striatus</i> Lea, 1913	5, 6
Curculionidae: Cryptorhynchinae: <i>Decilaus lateralis</i> Lea, 1913	6
Curculionidae: Cryptorhynchinae: <i>Decilaus</i> TFIC sp 04	? 8
Logging regeneration	
Carabidae: Carabinae: <i>Scopodes sigillatus</i> Germar, 1848	5, 8
Carabidae: Psydriinae: <i>Mecyclothorax ambiguus</i> (Erichson, 1842)	5, 8
Carabidae: Trechinae: <i>Cyphotrechodes gibbipennis</i> (Blackburn, 1901)	? 5
Carabidae: Agoninae: <i>Homethes elegans</i> Newman, 1842	? 5
Leiodidae: Leiodinae: <i>Zeadolopus</i> sp3	5, 8
Staphylinidae: Pselaphinae: <i>Anabaxis</i> CHANDLER 'Type 1'	5, 8
Staphylinidae: Pselaphinae: <i>Eupines</i> CHANDLER 'Tasmania 1'	8
Staphylinidae: Pselaphinae: <i>Euplec6</i>	8
Staphylinidae: Pselaphinae: <i>Rybaxis parvidens</i> Lea, 1911	5
Staphylinidae: Aleocharinae: Aleoc_10	8
Staphylinidae: Oxytelinae: <i>Anotylus</i> TFIC sp 04	8
Staphylinidae: Oxytelinae: <i>Anotylus</i> TFIC sp 03	8
Scirtidae: <i>Pseudomicrocara</i> TFIC sp 02	5
Byrrhidae: Byrrhinae: <i>Microchaetes scoparius</i> Erichson, 1842	5
Byrrhidae: Byrrhinae: <i>Pedilophorus mixtus</i> Lea, 1907	5
Sphindidae: <i>Aspidiphorus humeralis</i> Blackburn, 1894	? 8
Anthicidae: Anthicidae TFIC sp 02	? 5
Chrysomelidae: Galerucinae: <i>Arsipoda variegata</i> (Westwood, 1838)	5, 8

The edge-effects studies presented here showed that riparian-aligned wildlife habitat strips, and all width classes of streamside reserves, were likely to be entirely edge affected for ground-dwelling beetles. This was demonstrated to be the case for streamside reserve corridors of average width 40 ± 6 m ($\pm 95\%$ CI) from either side of reserve edges to streams. These results argue for wider wildlife habitat strips in riparian areas, and also for a much greater proportion of wildlife habitat strips to be located upslope. The current bias in southeast Australia towards locating corridors in gullies also fails to meet the habitat and dispersal requirements of some forest mammal (Claridge and Lindenmayer, 1994) and bird species (MacDonald et al., 2002). Upslope-positioned wildlife habitat strips should in theory contain interior habitat for ground-dwelling beetle species in wet forest, since edge effects were predicted to penetrate ~22 m into upslope habitat. Due to their unavailability in the study area, this could not be tested for wet eucalypt forest. However, upslope-positioned, 100 m wide wildlife habitat strips were not entirely comparable to continuous mature forest for ground-dwelling beetles in other Tasmanian ecosystems (Grove, 2004; Grove and Yaxley, 2005), suggesting that wider wildlife habitat strips may be preferable regardless of their landscape positioning.

Optimal reserve allocation strategies have been a source of debate amongst conservation biologists, as illustrated by the SLOSS debate over whether a given area is better allocated as a single large, or several small reserves (Diamond, 1975; Simberloff and Abele, 1982; Wilcox and Murphy, 1985). Ecological theory often provides potential arguments both in favour and against different options, suggesting that determining optimal reserve design is far from straightforward. Furthermore, an optimal design for ground-dwelling beetles may be sub-optimal for other taxa with different requirements. A key challenge to designing reserve networks for beetles

and other invertebrates is the lack of knowledge about the habitat requirements and distributions of most species. These issues argue for a mix of reservation approaches as part of the overall conservation strategy for Tasmania's production forests.

In finding the balance between wood production and conservation, limits to the overall area that can be allocated to reserves in production forests will necessitate some compromises in reserve allocation. For example, it may be better to have fewer wildlife habitat strips, but wider ones (e.g. 200 m wide), so that they are wide enough to support sensitive edge-avoiding species. Monitoring and adaptive management (Lindenmayer and Franklin, 2002) of reserves are needed. Further consideration should be made to the relative benefits of corridors versus patches for reserve allocation (Niemelä, 2001; Mönkkönen and Mutanen, 2003). Minimising edge to interior ratios (e.g. Laurance and Yensen, 1991; Sisk and Margules, 1993) is a common recommendation for the design of nature reserves, yet this is a particular issue with corridor reserves, because they inherently have a high proportion of edge habitat for their total area (Soulé and Gilpin, 1991; Hobbs, 1992). Thus allocating a proportion of reserve area into roughly circular-shaped blocks, representing both riparian and upslope habitats, could enhance the overall reservation system. The role of corridors in connecting otherwise isolated fragments is a common justification for this reservation strategy (Harris and Scheck, 1991; Soulé, 1991). Thus knowledge of the extent to which species use the corridors for dispersal is important, since if species are capable of dispersal across young regeneration, corridors may not be the most effective way of allocating hectares of forest into reserves (Hill, 1995; Beier and Noss, 1998; Niemelä, 2001). The present studies suggest certain beetle species specialised for mature forest may not readily disperse across regeneration habitat, although this needs confirmation. The influence of corridor length on habitat use and dispersal should also be considered (Bennett, 1990; MacDonald et al., 2002).

However, another benefit of corridors, in the light of high turnover of beetles among sites, is that this reserve strategy may be more effective at conserving habitat across the landscape relative to apportioning an equivalent area into contiguous blocks. Rare species are among the most sensitive to habitat loss and fragmentation, and therefore may benefit most from an effective reservation strategy (Soulé, 1991; Davies et al., 2004). Managing for rare invertebrate species is challenging, and more often than not hindered by lack of knowledge of species' distributions and habitat requirements. Using a mixed approach to reserve allocation could therefore be a good risk management strategy.

The degree to which legislation such as the Forest Practices Code (Forest Practices Board, 2000) needs to be prescriptive is worth consideration. In many respects, a more flexible approach to forest management could have ecological benefits, for example one of the areas in which logging currently fails to mimic the natural wildfire regime is with respect to variability, for example in coupe sizes and age distributions (Baker et al., 2004). As previously discussed, a flexible and variable approach to allocation of reserves in logging areas could have benefits. On the other hand, pressure to meet timber quotas from the limited available area of State Forest means that the distinction between prescriptions and recommendations in the Forest Practices Code becomes important. One example is the wording relating to the positioning of wildlife habitat strips. According to the Forest Practices Code (Forest Practices Board, 2000), "Wildlife habitat strips should be retained to maintain habitat diversity. As a guide, strips of uncut forest 100 m in width, based on streamside reserves but including links up slopes and across ridges to connect with watercourses in adjoining catchments, should be provided every 3-5 km. These strips should connect any large patches of forest which are not to be harvested, such as formal and informal reserves." The flexibility in wording can result in failure to achieve the

intended outcomes. In the Geeveston District State Forest, where the present studies were conducted, the wildlife habitat strip network is almost entirely positioned as widened streamside reserves (i.e. in riparian areas). It is easy to understand how such a situation may arise, since widening Class 3 streamside reserves by 40 m would result in much less area lost to production than would leaving 100 m wide strips away from riparian areas. Therefore a more prescriptive approach to ensuring the retention of linkages up slopes and across ridges should be considered.

One of the great challenges of conservation management planning is the incorporation of ecological complexity and uncertainty (Burgman et al., 2005; Fischer and Lindenmayer, 2006). These constraints are well illustrated by the challenge to ensure forest management practices do not have negative consequences for ground-dwelling beetle biodiversity. Making pragmatic recommendations for a conservation strategy that will conserve biodiversity in forestry areas, but that will also be feasible from economic and silvicultural standpoints, is far from straightforward. These studies illustrate that beetle responses to forest management practices are species-specific. The notion that species respond individualistically to the environment can be incorporated via a range of approaches into landscape management planning for conservation (e.g. Burgman et al., 2005; Moilanen et al., 2005; Fischer and Lindenmayer, 2006). The continuum model approach described by Fischer and Lindenmayer (2006) allows incorporation of information about environmental gradients such as edge or riparian effects into habitat suitability modelling. This is an advance on the fragmentation model approach, that assumes clear contrast between habitat patches and an uninhabitable matrix, without taking into account differing species-specific perceptions of suitable habitat (Fischer and Lindenmayer, 2006). Nevertheless, such models are largely conceptual. Strategies such as reserve selection algorithm and gap analysis approaches also have their

limitations, and may not be as readily applicable to reserve planning for invertebrate communities. These approaches have generally been applied using habitat types as surrogates, or for species such as many higher plants or vertebrates for which detailed background information about habitat requirements and/or distributions are often available (Margules et al., 1988; Margules et al., 1994; Pressey et al., 1996; Lindenmayer and Burgman, 2005). Unfortunately using vegetation type as a surrogate for beetle biodiversity also may not be effective (Oliver et al., 1998; Panzer and Schwartz, 1998; Mac Nally et al., 2002). The continuum model (Fischer and Lindenmayer, 2006) has some parallels with the natural disturbance model (Baker et al., 2004), in that they both recommend heterogeneity at both landscape and microhabitat scales. The continuum model suggests that because of species-specific differences, no single conservation action can benefit all species (Fischer and Lindenmayer, 2006). This again argues for applying a variety of both reserve design and silvicultural strategies across forest management planning units.

Directions for future research

The studies described in this thesis are among relatively few Tasmanian studies that have investigated factors affecting the distributions of ground-dwelling beetle species. The studies demonstrate that beetle responses are largely species-specific, and importantly, that patterns could not necessarily be predicted from beetle distributions or responses to environmental gradients in other ecosystems. This thesis has just scratched the surface in terms of understanding the habitat preferences of beetles and their sensitivity to forest management, but it has also suggested many potentially worthwhile research pathways. General areas that seem particularly worthy of future research effort relate to taxonomy and basic ecology, determining

what proportion of overall habitat, and at what spatial scale, is required for effective reservation, and determining the affects of various temporal factors on beetle assemblages and reservation effectiveness. Efforts to fill in these knowledge gaps should provide information to improve our ability to effectively plan for conservation of ground-dwelling beetle biodiversity in production forests.

Taxonomy and habitat requirements

In contrast to the relatively well known beetle fauna in European forests, the ‘taxonomic impediment’ is of serious concern in Australian studies. Many beetle species have not yet been described taxonomically, and named reference specimens of many species are not yet lodged in the Tasmanian Forest Insect Collection; these are topics that are being addressed on an ongoing basis, but are still a limitation to conservation biology for beetles in Tasmania. Larvae have not been identified for the majority of forest beetle species and virtually nothing is known of their requirements. However, Yee’s (2005) study indicated that a proportion of species that inhabit the litter-layer as adults (this thesis) use logs for larval development. Since beetles may potentially disperse through corridors over the course of several generations, the effectiveness of reserves for larval habitat is also needs considering. Further studies to determine the general habitat requirements and ecology of individual beetle species would be worthwhile. Such knowledge might help identify species that are potentially at risk from current management practices (e.g. Didham et al., 1998; Davies et al., 2000; Henle et al., 2004). However, a species level-approach to conservation of the majority of ground-dwelling beetle species is not going to be realistic in the immediate future.

Reserve area requirements and spatial distribution

It is not presently known how well represented most beetle species are in the large areas of wet eucalypt forest reserved from harvesting in National Parks and permanent Forest Reserves within State Forest. Large intact areas of forest not subject to fragmentation by roads and harvesting-related changes to the natural age-structure and patch-size dynamics are potentially very valuable for conservation. However, high assemblage turnover among sites, known localised ranges for some beetle species, and the species-area relationship, suggest that some beetle species may not be well represented in these larger reserves. Future research could assess the proportion of wet forest beetles that have viable populations within National Parks and other large formal reserves. Better documentation of species distributions and population densities is required. Studies comparing beetle populations in formal reserves to commercial forests could also assess effects of habitat loss, and habitat fragmentation per se (sensu Fahrig, 2003), on beetle communities, including the importance of area effects. Although difficult, particular consideration should be given to rare species.

Within State Forest, biodiversity conservation efforts would be aided if research were able to provide ‘rules of thumb’ for the proportion of old-growth habitat needed to maintain viable populations, in conjunction with guidance about the minimum area requirements and spatial scales of distribution of habitat that are required. Habitat loss is probably among the most important potential extinction threats for forest biodiversity (Tilman et al., 1994; Lindenmayer and Franklin, 2002; Fahrig, 2003). Estimates of “extinction threshold” levels of habitat loss and fragmentation (Wilcove et al., 1986; Fahrig, 2003; Solé et al., 2004) could in theory provide an easy to interpret guide for conservation planners, but unfortunately there is currently little basis to make such estimates, which would inevitably be ecosystem-

and species-specific. More research into this subject could be of substantial benefit; for example, identifying which species are most vulnerable to habitat loss and fragmentation, and then estimating the minimum habitat requirements to ensure their persistence (Fahrig, 2003). With better data on species' distributions, it may be possible to conduct Population Viability Analyses (Possingham et al., 1993) for species found to be sensitive to edge and area effects or other potential threats associated with forest management. Integrating studies of beetle ecology and landscape ecology with GIS tools, and use of genetic techniques to assess dispersal capabilities of potentially sensitive target species, could provide a means of exploring fragmentation effects, an area of conservation biology that has received very little research attention in Tasmania. Beetles' sensitivity to area effects is an important knowledge gap concerning their sensitivity to fragmentation that has implications for the ecological consequences of forest harvesting. Estimates from this thesis of the depth of penetration of edge effects into riparian and non-riparian habitat could be integrated with GIS tools to assess landscape-scale impacts of different harvesting scenarios. The added value that could be provided by estimates of the area requirements of sensitive species cannot be overstated. Although costly to establish, a landscape fragmentation experiment in the style of the Brazilian Biological Dynamics of Forest Fragments Project or the Australian Wog Wog and Tumut fragmentation experiments could make an enormous contribution to our understanding of fragmentation ecology in Tasmania (Bierregaard et al., 1992; Margules, 1992; Lindenmayer, 2000).

Temporal factors

It is possible that habitat loss and fragmentation over recent decades have been creating what conservation biologists describe as an "extinction debt", where time

lags before regional extinction mean that some species presently occurring in forestry areas might be at risk of extinction in the future (Tilman et al., 1994; Hanski and Ovaskainen, 2002; Ewers and Didham, 2006). Reviews of fragmentation studies indicate that while short-term studies are more likely to detect crowding effects, more severe long-term consequences such as reduced species richness and/or population density may not immediately be apparent because of time lags (Debinski and Holt, 2000; Ewers and Didham, 2006). Based on simulation modelling, even abundant and competitively dominant species are predicted to be at risk of extinction caused by habitat loss and fragmentation (Tilman et al., 1994). Hanski and Ovaskainen (2002) provide an example from Finnish forests where more regionally extinct beetle species were found in regions with longer management histories. Tasmanian forestry areas are currently analogous to more recently exploited Finnish forests, suggesting that future extinctions caused by intensive management are a possibility. It therefore seems important that we assess whether current and past management practices are posing an extinction risk for forest biodiversity, and take remedial action if this is the case (Hanski and Ovaskainen, 2002).

This thesis assessed relatively short-term responses of ground-dwelling beetles to forest management practices. It would be useful to determine the time frame over which regeneration forest becomes suitable, both as habitat and to enable dispersal, for sensitive mature forest species. Long-term studies should also investigate whether edge effects dissipate with time. Investigation of tree death and windthrow at reserve edges relative to continuous forest interior could confirm whether there is increased tree death at the edges of reserves (e.g. Kapos et al., 1997; Laurance et al., 2002; Hylander et al., 2004) and estimate rates of edge-creep. If reserve edges encroach into the reserve through time, then relatively narrow reserve corridors may rapidly lose integrity and habitat quality over successive harvesting

rotations. A better understanding of temporal processes may be particularly important in assessing the long-term viability of reserve corridors and smaller reserve areas. Two possible general scenarios are: i) as the logged forest ages, edge effects may become less pronounced, and the matrix more usable for many species, hence the reserves may provide better habitat than they do currently; or ii) time-lags in species' responses to habitat loss and fragmentation (Ewers and Didham, 2006), and gradual windthrow of retained trees and associated changes to habitat conditions at ground level, may result in the degradation of reserves over time.

The long-term management of reserves with respect to their future regeneration needs to be considered, since wildfire is the main natural regeneration process in this forest type, but forest management practices include a fire prevention policy. Allowing some reserves to be burnt when adjacent coupes undergo regeneration burns could be considered, although is probably a risky strategy with respect to the overall fire prevention policy. However, the propensity for some regeneration burns to escape over coupe boundaries into adjacent unlogged forest could actually be fortuitous in resolving this issue.

Conclusions

Ground-dwelling beetles were found to be sensitive to various habitat factors in a managed wet eucalypt forest ecosystem. Beetles were responsive to forest age, showed spatial patterning among study sites, and patterns in species richness, abundance and assemblage composition in response to riparian gradients and edge effects from clearfelled logging coupes. Further, an interaction between edge and riparian influences caused deeper penetration of edge effects for beetles into riparian than upslope habitat. Based on these findings, current width prescriptions for

streamside reserves and riparian-positioned wildlife habitat strips are predicted to be inadequate for providing a core area of habitat not subject to edge effects on ground-dwelling beetles. This prediction was confirmed in a study of streamside reserves that had been logged on both sides, and were not of equivalent habitat value for beetles to continuous forest. These findings suggest that loss of mature forest habitat in successive rotations of native forest logging may have negative consequences for the beetle species dependent on this forest type. Documenting an edge-response by beetles, and in particular detecting some edge-avoiding mature forest specialists, is evidence that fragmentation is acting on beetles in this ecosystem. However, improved networks of reserve corridors have the potential to mediate these effects. It is recommended that wildlife habitat strips be wider, and more often positioned upslope. Wider reserves, e.g. 200 m wide wildlife habitat strips, more frequent positioning of habitat strips upslope (e.g. 50%), and apportioning some reserve area allocation as habitat blocks rather than corridors, could be implemented in an adaptive management framework combined with monitoring and additional research targeting current knowledge-gap areas. Further studies of spatial and temporal factors in relation to population persistence of ground-dwelling beetles in production forestry areas are recommended as part of this adaptive management framework.

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Appendix 1

Pilot study

Aims

A small pilot study was conducted prior to establishment of Trial 1. The aims of the pilot study were to provide information to assist trial design with regards to:

- a) distances between pitfall traps in transects in order to identify the width of the riparian zone for the beetle fauna.
- b) whether beetle assemblages on sedimentary derived soils were similar enough to those on dolerite derived soils to allow use of both landforms for study sites; since of the five sites identified as potentially suitable for Trial 1, three were on dolerite and two were on sedimentary derived soils.

Methods

The pilot study was set up on 21-22 January 2001. One pitfall trap transect was established in streamside reserves at each of three sites. Two dolerite (WR011B and PC073A) sites and one sedimentary (PC24A) site were used. Pitfall traps were placed at distances of 1 m, 2 m, 3 m, 4 m, 5 m, 6 m, 7 m, 8 m, 9 m, 10 m, 15 m, 20 m and 25 m from the stream with an additional trap placed at the edge between the coupe and the streamside reserve. Five centimetre depth bulk density cores were collected from each pitfall trap location to allow calculation of soil moisture content. Traps were left open for four weeks (collected on 20 February 2001); examination after two weeks indicated that there were insufficient beetles.

All Coleoptera were removed from pitfall traps and identified to morphospecies. The abundances of each morphospecies at each trap were entered

into Microsoft Excel, and data imported into PATN for multivariate analysis. In total, 557 beetles from 98 morphospecies were trapped. Non-metric multidimensional scaling ordination of data were conducted based on common morphospecies; i.e. species for which four or more individuals were trapped (approximately 1% of the total catch). 457 beetles from 26 morphospecies and 10 families were included in these analyses (see Table 1).

The percentage moisture content was calculated for soil samples after oven drying at 105°C.

Results

Patterns in beetle assemblage composition in an ordination of presence-absence data (not presented) were similar to those from the ordination using abundance data (Figure 1). Examination of the ordination of beetle abundances (Figure 1), suggested that at WR011B, the trap 1 m from the stream was positioned separately from other distances from the stream and edge. At PC073A, traps located at 1 m and 15 m from the stream, and the trap at the habitat boundary between the coupe and the streamside reserve are positioned separately. Plots from PC024A showed greater overall scatter than the other two sites, but plots 1 m from the stream and at the streamside reserve edge appeared not to be clustered separately, although the trap at 9 m from the stream appeared to have somewhat different beetle assemblage composition. Based on these results, there is some indication that beetle communities immediately adjacent to streams, and at the streamside reserve edge, may be of different assemblage composition than the remainder of the beetle assemblage in the streamside reserves. However, no other relationships were apparent with distance

from stream. Edge traps and traps located 1 m from streams at the three sites were not clustered together, indicating site-specific responses.

Percentage soil moisture content did not appear to be related to distance from the streams (Figure 2).

Site PC073A (dolerite) is clustered more distinctly relative to the other two sites, with greater overlap in beetle assemblage composition evident between PC024A (sedimentary) and WR011B (dolerite). Therefore site differences in beetle assemblage composition do not appear to relate to soil type.

Conclusions

With regards to the distance between traps in transects at right angles to streams, these results indicated that the only distinction in assemblage composition appeared to be at 1 m from the streams, hence a trap should be located at this distance in Trial 1. Beyond 1 m, it does not appear to be necessary to have traps at each metre from the stream, thus sampling effort could be allocated as seems reasonable based on other considerations.

These results suggest that trapping on both dolerite and sedimentary landforms would be appropriate in Trial 1.

Table 1. Number of beetles of each common (≥ 4 beetles) morphospecies trapped in streamside reserves at three sites.

Morphospecies	Site			Total
	PC073A	PC024A	WR011B	
Carabidae: <i>Chylinus ater</i>	6	1	3	10
Carabidae: <i>Promecoderus longus</i>	5	0	0	5
Carabidae: <i>Rhabdotus reflexus</i>	12	2	0	14
Carabidae: <i>Sloanella</i> sp.1	0	0	5	5
Leiodidae: <i>Nargomorphus</i> sp.1	2	1	1	4
Leiodidae: <i>Choleva</i> TFIC sp 01	0	9	17	26
Leiodidae: <i>Austronemadus</i> TFIC sp 03	51	2	11	64
Aleocharinae: Aleoc_1	17	23	36	76
Aleocharinae TFIC sp 02	6	0	1	7
Aleocharinae: Aleoc_37	32	5	12	49
Aleocharinae: Aleoc_41	4	0	0	4
Aleocharinae: Aleoc_44	7	0	7	14
Aleocharinae: Aleoc_50	0	2	6	8
Lucanidae: <i>Lissotes</i> nr. <i>bornemisszai</i>	2	6	0	8
Lucanidae: <i>Lissotes</i> sp.	1	0	6	7
Byrrhidae: <i>Pedilophorus multicolor</i>	0	6	3	9
Byrrhidae: <i>Microchaetes hystricosus</i>	5	1	8	14
Nitidulidae: <i>Thalycrodes cylindricum</i>	3	10	0	13
Lathridiidae: <i>Aridius nodifer</i>	36	9	16	61
Curculionidae: <i>Decilaus nigronotatus</i>	2	1	2	5
Curculionidae: <i>Decilaus</i> TFIC sp 01	1	1	11	13
Curculionidae: Crypt_4	0	5	6	11
Curculionidae: <i>Decilaus lateralis</i>	1	1	8	10
Curculionidae: Curcul_9	0	3	7	10
Sphindidae: <i>Aspidiphorus humeralis</i>	4	1	1	6
Phloestichidae: <i>Hymaea</i> sp.	0	0	4	4
Grand total			457	

Figure 1. 3-dimensional ordination of beetle assemblages at three sites and 14 distances from streams. Triangles are PC024A, squares are PC073A and crosses are WR011B sites. For 1 m plots and outlier plots, distance from streams is indicated in m; E refers to the streamside reserve edge. Stress = 22%.

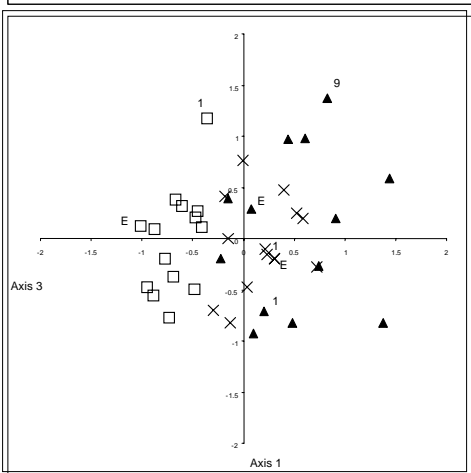
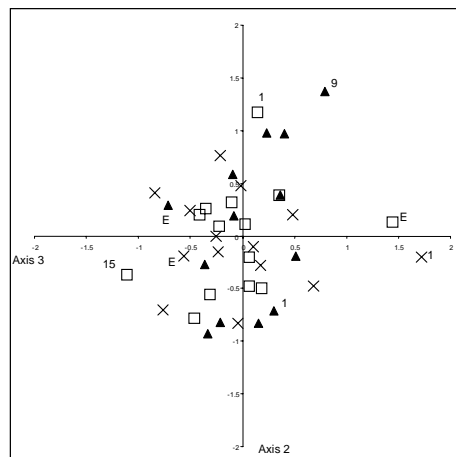
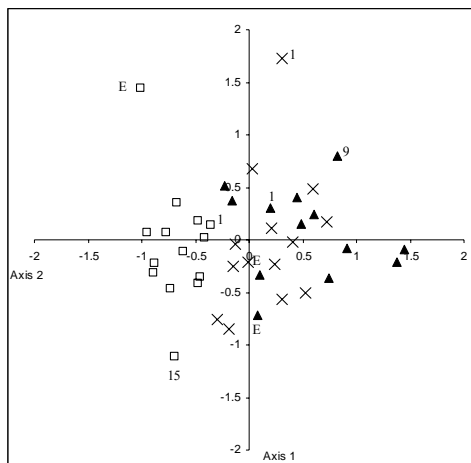
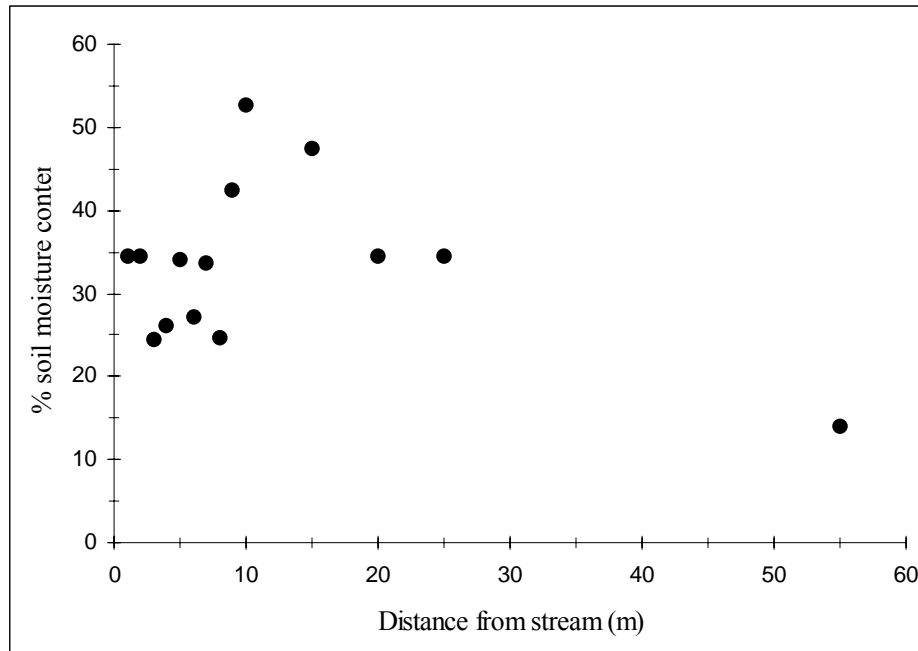


Figure 2. Plot of percentage soil moisture content with distance from stream at the three study sites.



Appendix 2

Allocation of sampling effort in Trial 2

Aims

Available existing ground-dwelling beetle datasets from the same study region were screened to assist allocation of sampling effort in Trial 2 (Chapter 8). It was intended that Trial 2 would collect beetles in four treatments (habitats), and the total number of pitfall traps would be constrained to 300-400 traps. The aims of the preliminary data analyses were to estimate the minimum number of traps required per stand, and to guide allocation of sampling effort between levels in the proposed nested study design (traps within transects within stands).

Methods

Two datasets were available for data screening. These were data from a comparison of ground-dwelling beetles in 33-year old clearfelling and wildfire regeneration in the Arve River valley (Baker 2000; Baker et al. 2004), and data from the first two sampling periods (winter and spring) from Trial 1 of this thesis. Two analysis approaches were taken in examining these datasets.

Species accumulation curves were created using the ‘species-area curves’ function in PC-ORD Version 4.10 (McCune & Grace 2002; McCune & Mefford 1999). These analyses were based on data for commonly collected species, and were intended to assist determining the number of traps required per stand to collect the majority of common beetle species.

Nested ANOVA in Systat was conducted to enable examination of the relative variance components (Sokal & Rohlf 1995) associated with different levels

of nesting in the study designs; i.e. between the levels: sites, transects or plots within sites, and traps within transects or plots. This analysis assists in best allocating available trapping units to effectively sample variation at different spatial scales. For the Arve River valley dataset, this was conducted for total species richness, total and common species abundance, and the abundance of three commonly collected taxa, the Carabidae, Aleocharinae, and Curculionidae. For the Trial 1 dataset, analyses were conducted separately based on the abundance of 33 common species, and mean variance at each level in the design calculated.

Results

Based on variance components analysis (Figures 1 and 2), the majority of variation in pitfall trap catches was at the trap-to-trap level within transects or plots. Stand level variation was next most important, and the lowest proportion of variation was explained at the transect or plot level.

Species accumulation curves (Figures 3 and 4) indicated that 18 pitfall traps collected between approximately 80% and 90% of common beetle species. As many as 40 traps may be required to collect 95% of beetle species.

Figure 1. Variance components analysis for levels of nesting in a study of ground-dwelling beetles in the Arve River valley. The percentage of total variance at the site, plot and trap level is presented for total species richness (S) and five indices of beetle abundance (N).

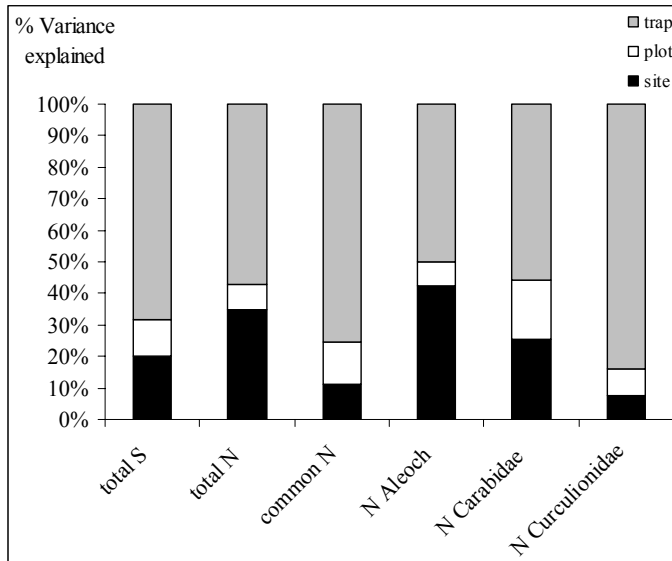


Figure 2. Variance components analysis for sampling levels in Trial 1 of this thesis. The average percentage of total variance at the site, treatment, transect and trap levels are presented based on analyses of the abundance of the 33 most common beetle species.

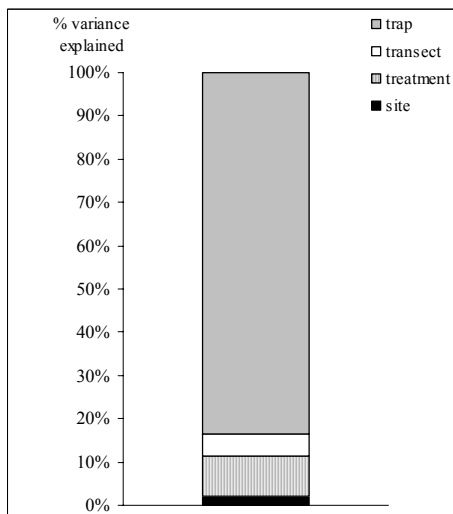


Figure 3. Species accumulation curve of the abundance of commonly collected beetles in the Arve River Valley.

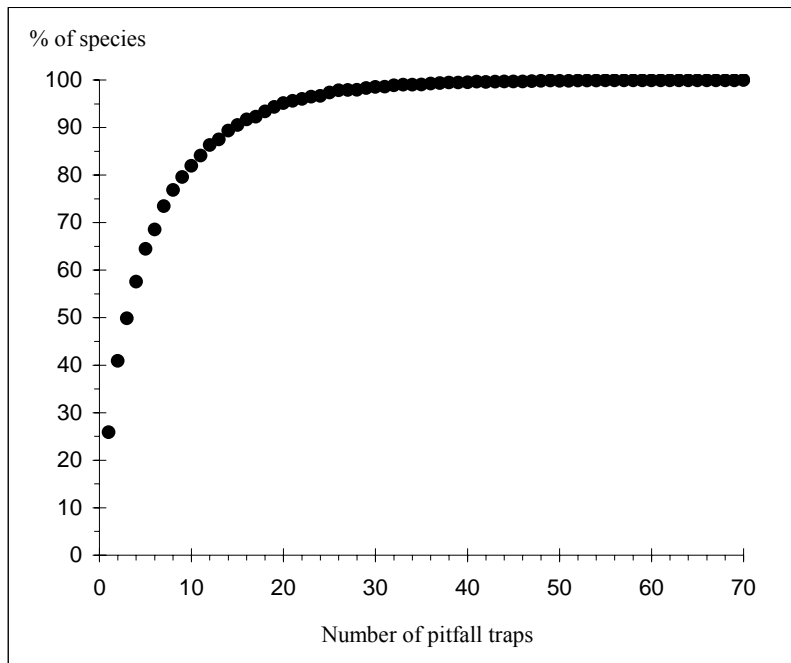
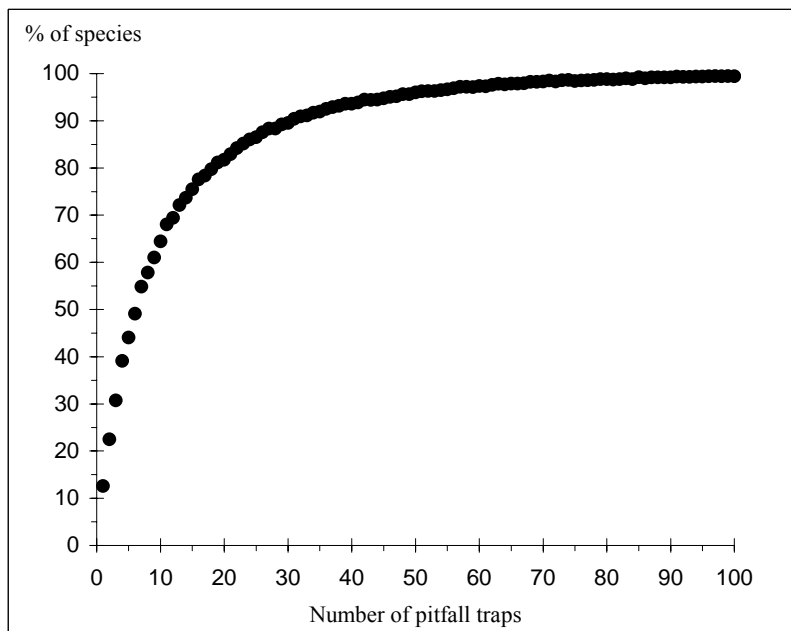


Figure 4. Species accumulation curve of the abundance of commonly collected beetles from winter and spring sampling in Trial 1 of this thesis.



Conclusions

These results suggest that the majority of variation in pitfall trap catches of ground-dwelling beetles was occurring at the trap-to-trap level. Allocation of sampling effort should therefore be biased in favour of the number of traps in transects, then towards numbers of stands, with least emphasis on the number of transects within stands. A total of 18 traps per stand are probably sufficient to collect 80-90% of commonly occurring ground-dwelling beetle species. Hence a sampling design was conceived consisting of five replicate stands of each of the four treatments, with three transects of six pitfall traps each per stand ($5 \times 4 \times 3 \times 6 = 360$ traps).

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Appendix 3

Extra riparian analyses

Indicator species analysis of beetles in riparian compared to upslope habitat

Aims

An indicator species analysis was conducted with the objective of determining whether any of the commonly collected beetle species in Trial 1 could be classified as characteristic of riparian or upslope habitats. This analysis was intended to complement the analyses presented in Chapters 3 and 4, which did not detect any beetle species that appeared to be specialized to riparian or upslope habitats.

Methods

Indicator species analysis (Dufrêne & Legendre 1997) conducted in PC-ORD Version 4.10 (McCune & Grace 2002; McCune & Mefford 1999) assessed the habitat preferences of individual beetle species for the riparian and upslope areas in continuous mature forest. Unlike the statistical approaches taken in Chapter 4, indicator species analysis is able to assess habitat preferences of species that were collected much less commonly. The approach uses average abundance at the site level of beetles in the habitats of interest. Thus, although Chapters 3 and 4 found riparian zone width to vary among the four study sites in Trial 1, the indicator species analysis categorised particular distances from the streams as either ‘riparian’ or ‘upslope’ habitats across the four sites. Hence, traps from 1 m, 5 m, and 10 m from streams in riparian transects were used to represent the riparian zone, and the same three traps from mature upslope transects were used to represent upslope

habitat. The analysis used mean abundances per stand (4 site replicates) for beetle species collected ≥ 10 times. Indicator species analysis combines information about species' relative abundance (specificity) and relative frequency of occurrence (fidelity) in each habitat to calculate an Indicator Value (IV, %), where 0% represents no indication and 100% represents perfect indication of that habitat. A Monte Carlo P -value (9999 permutations) evaluated the statistical significance of the IV for each species.

Results

Only one beetle species was found to be significant in this analysis (Table 1). The carabid *Promecoderus longus* was significant ($P = 0.0290$) for riparian habitat, but this is probably of spurious significance (Type I error) based on the species' known distribution in upslope areas from the entire PhD dataset, and previous research (Taylor et al. 2000). All other species were of $P > 0.1$, including *Microsilpha* 'ANIC Thayer sp 15' which although it was only of IV = 1 in upslope habitat in this analysis, was also relatively common in upslope areas from the entire PhD dataset from which it was primarily collected at the Kermandie site.

Conclusion

The results of this analysis agree with other analyses from Trial 1, that none of the commonly collected beetle species were specialised to riparian or upslope habitats.

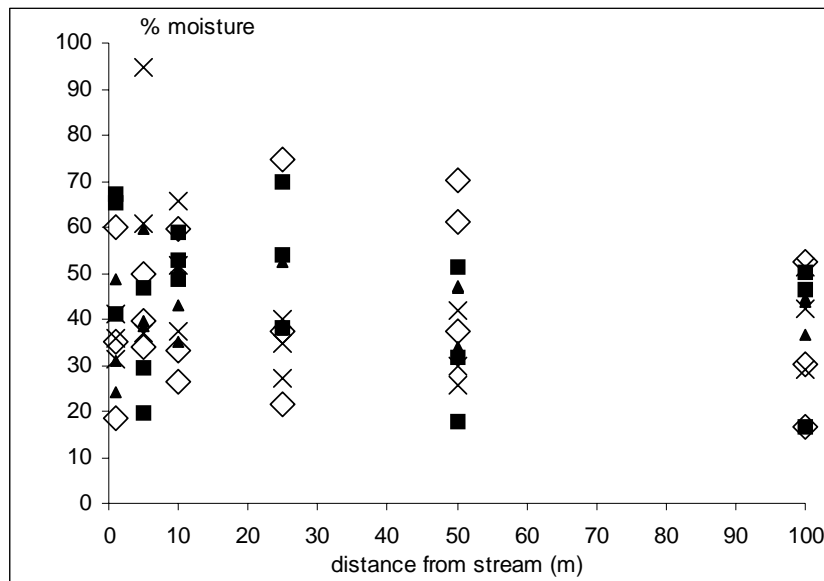
Table 1. Results of indicator species analysis comparing riparian and upslope habitats.

Morphospecies	IV riparian	IV upslope	IV overall	P value
<i>Adelium abbreviatum</i>	38	12	38.1	0.8849
Aleocharinae TFIC sp 02	43	43	43.2	1
Aleocharinae: Aleoc_1	54	46	54.2	0.8860
Aleocharinae: Aleoc_16	23	55	55	0.4311
Aleocharinae: Aleoc_37	23	35	34.6	0.9149
<i>Austronemadus</i> TFIC sp 03	44	56	56.3	0.5456
<i>Baeocera</i> TFIC sp.02	28	47	47.4	0.7717
<i>Choleva</i> TFIC sp 01	27	73	72.7	0.7138
Cryptorhynchinae TFIC sp 07	25	33	33.3	1
Cryptorhynchinae: Crypt4	53	15	52.5	0.4022
Curculionidae sp.28	15	35	35	0.6577
<i>Decilaus lateralis</i>	53	7	52.5	0.3718
<i>Decilaus nigronotatus</i>	49	51	50.9	1
<i>Decilaus striatus</i>	49	51	51.4	0.9446
<i>Decilaus</i> TFIC sp 01	15	53	52.9	0.4865
<i>Decilaus</i> TFIC sp 04	54	14	54.2	0.4026
<i>Lissotes</i> nr. <i>bornemisszai</i>	27	23	27.3	1
<i>Mandalotus muscivorus</i>	58	32	57.9	0.6277
<i>Microsilpha</i> 'ANIC Thayer sp 15'	48	1	48.1	0.4306
<i>Nargomorphus</i> sp.1	41	59	58.8	0.7150
<i>Nargomorphus</i> sp.2	15	20	20.2	1
<i>Nargomorphus</i> TFIC sp 05	9	41	40.9	0.5440
<i>Notonomus politulus</i>	22	42	42	0.7448
<i>Orchesia alphabetica</i>	41	59	59	0.4024
Oxytelinae: Oxytel2	13	12	13.5	1
<i>Promecoderus longus</i>	79	21	79.3	0.0290
<i>Pselaphaulax</i> CHANDLER 'Tasmania 1'	78	17	77.8	0.2022
<i>Quedius</i> 'ANIC Newton sp03'	12	53	53.3	0.3988
<i>Rhabdotus reflexus</i>	30	45	45.5	0.9165
<i>Roptoperus tasmaniensis</i>	52	48	52.4	0.8870
Scydmaenidae sp. 2	14	61	60.9	0.3133
<i>Sloaneana tasmaniae</i>	22	53	52.6	0.6271
Sogdini 'ANIC gen B' TFIC sp 01	27	34	34.1	0.8287
Staphlyninae TFIC sp 03?	16	34	34.1	0.8861
<i>Startes</i> CHANDLER 'Tasmania I'	59	11	58.9	0.2875
<i>Stichonotus leai</i>	20	45	45	0.6591
<i>Tasmanityrus newtoni</i>	40	10	40	0.5400
<i>Thalycrodes cylindricum</i>	4	63	62.5	0.2576

Soil moisture content in riparian-upslope transects

Elevated moisture content is a common characteristic of riparian areas, and therefore might be expected to also influence ground-dwelling beetle distributions. The relationship of soil moisture with distance from streams is relevant to Chapter 3 of this thesis. Soil moisture content did not appear to be related to distance upslope from the streams (Figure 1). Although this data is confounded somewhat by rain events between sampling (see Methods, Chapter 3), there were no trends relating to distance from stream within sites. It therefore appears that soil moisture is extremely variable, and contrary to expectation, does not appear to be greatest nearer the streams.

Figure 1. Soil moisture (%) at pitfall trap locations plotted against distance from stream at each study site. Squares are Isabell Creek; triangles are King Creek; crosses are Leas Creek; diamonds are Critter Creek.



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Appendix 4

Seasonality of edge response in riparian transects

Aim

There is potential for the depth of penetration of edge effects to vary seasonally, since beetles' edge response may be partially related to microclimatic gradients in habitat conditions. Preliminary data analyses of beetle assemblage response to edge effects were conducted with the objective of determining whether beetles' edge response shifted seasonally with the three pitfall trapping periods (winter, spring, summer-autumn). Results for non-riparian edges are presented in Chapter 6 and results for riparian transects are presented here.

Methods

Non-parametric multivariate analysis of variance (NPMANOVA, Anderson 2001, 2003) was used to test beetle assemblages for a multivariate interaction between "season" and "distance from edge" at each site, using a two-way crossed model. Non-riparian and streamside reserve edges were also analysed separately, since transect lengths differed between these edge types. For streamside reserve transects, "Season" (winter, spring, summer-autumn samples) and "Distance" (-10 m, -5 m, 1 m, 5 m, 10 m, 25 m and 50 m from edge) were fixed factors. Negative distances indicate locations in the coupe firebreaks. The 50 m category was unavailable for Manuka and Kermandie streamside reserves, because of reserve widths. These analyses were conducted on square-root transformed abundance data using Bray-Curtis dissimilarities and 9999 unrestricted random permutations of the raw data, where the three transects at each edge were considered replicates. Rare species (those

recorded only from single samples or of abundance less than 0.5% of the total abundance) were omitted. There were 41 common morphospecies for Picton, 23 for Warra, 37 for Manuka, and 36 for Kermandie.

Results

Streamside reserve edge transects

At none of the four streamside reserves was there a significant interaction between distance from the coupe edge and season (Table 1), indicating that the edge response was also not shifting seasonally in riparian habitat. Beetle assemblage composition was found to vary seasonally at Picton, Manuka and Kermandie streamside reserve edges, while season was not significant at Warra.

At Picton and Manuka, pairwise comparisons found the beetle assemblages from each season to differ significantly from the other seasons. At Kermandie, winter and spring beetle assemblages were not significantly different ($P = 0.184$) while summer-autumn assemblages differed significantly from both winter and spring ones ($P = 0.0001$).

Conclusions

The interaction between season and distance from coupe edges was found to be non-significant for streamside clearfelled logging coupe edges. Beetle assemblage composition did differ seasonally; however, these results suggest that the penetration of edge effects does not shift seasonally. Therefore, analysis of edge effects on beetles in Chapter 7 used pooled data from the three pitfall trapping periods.

Table 1. NPMANOVA testing for differences in ground-dwelling beetle

assemblages at streamside reserve coupe edges at Picton, Warra, Manuka and Kermandie sites over three seasons and either seven (Picton and Warra) or six (Manuka and Kermandie) distances from coupe edge.

Source	d.f.	SS	MS	F	P
<i>Picton</i>					
Distance	6	37927.36	6321.227	1.922	0.0002
Season	2	44012.08	22006.04	6.691	0.0001
Distance x Season	12	47682.29	3973.524	1.2082	0.0687
Residual	42	138134.7	3288.921		
Total	62	267756.4			
<i>Warra</i>					
Distance	6	41574.43	6929.072	1.6915	0.0039
Season	2	7121.152	3560.576	0.8692	0.6176
Distance x Season	12	43802.34	3650.195	0.8911	0.7697
Residual	42	172049.5	4096.416		
Total	62	264547.4			
<i>Manuka</i>					
Distance	5	34091.8	6818.36	1.9325	0.0002
Season	2	21685.52	10842.76	3.0731	0.0002
Distance x Season	10	43041.92	4304.192	1.2199	0.0762
Residual	36	127018.5	3528.291		
Total	53	225837.7			
<i>Kermandie</i>					
Distance	5	23267.64	4653.527	1.2796	0.0843
Season	2	22576.2	11288.1	3.104	0.0001
Distance x Season	10	29518.3	2951.83	0.8117	0.9127
Residual	36	130916.9	3636.58		
Total	53	206279			

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Appendix 5

Association of common brown froglets, *Crinia signifera*, with clearcut forest edges in Tasmania, Australia

This chapter previously published as:

Baker, S. and Lauck, B. (2006). Association of common brown froglets, *Crinia signifera*, with clearcut forest edges in Tasmania, Australia. Wildlife Research 33: 29-34. Note equal contribution of both authors.

Abstract

We examined the response of the common brown froglet, *Crinia signifera*, to recently clearcut forest edges in Tasmanian wet *Eucalyptus obliqua* forest. We established transects of pitfall traps crossing coupe edges, within coupes, and within mature forest interiors (riparian and non-riparian) at three study sites. Pitfall captures of *Crinia signifera* were greatest at the immediate logged forest edge (which corresponded with a firebreak constructed as part of standard clearfell, burn and sow silvicultural practices in Tasmania). Capture rates were lower in both the coupe interior and the immediate unlogged forest edge and declined to negligible numbers in the unlogged forest interior. Edge penetration was estimated to be generally 50-100 m. We suggest that Tasmania's current management of wet forest may provide additional habitat for *C. signifera* by changing the age structure of the forest and providing additional forest edge/firebreak habitat. However, *Crinia signifera* is common and disturbance tolerant, and thus these findings should not be extrapolated to other Australian frog species that may be disadvantaged by current logging practices.

Introduction

The term ‘edge effects’ describes biotic and abiotic changes that occur as a consequence of the juxtaposition of two different habitat types (Murcia, 1995; Schlaepfer and Gavin, 2001). Human activities have strongly influenced the extent and type of forest edges found on earth (Laurance and Yensen, 1991; Kapos et al., 1997). Worldwide, many studies have illustrated various responses of animals to clearcut forest edges: some animals are edge avoiders (and may be affiliated with clearings or with mature forest), others are attracted to edges, and other generalist species are unaffected by edges (Sisk and Margules, 1993; Murcia, 1995; Laurance et al., 1997; Didham et al., 1998; Matlack and Litvaitis, 1999).

Toral (2002) considered that changes in vegetation structure and microclimate are likely to be the predominant determinant of amphibian abundances across edges. Abiotic changes that commonly occur near edges include reduced soil moisture and humidity, higher solar radiation, more extreme temperatures, and greater wind disturbance than in the forest interior (Kapos et al., 1997; Turton and Freiburger, 1997; Lehtinen et al., 2003). Amphibians have physiological characteristics such as ectothermy and the possession of moist, permeable skin (Blaustein et al., 1994; Tyler, 1994; deMaynadier and Hunter, 1995) that may render them vulnerable to such microclimatic differences across edges (Toral et al., 2002). The edge response of amphibians in other studies is variable and emphasises the need for species- and habitat-specific studies to contribute to conservation planning (Gascon, 1993; Marsh and Pearman, 1997; deMaynadier and Hunter, 1998; Gibbs, 1998; Schlaepfer and Gavin, 2001; Toral et al., 2002; Lehtinen et al., 2003).

The common brown froglet, *Crinia signifera* (Girard 1853), is a small frog with an average adult snout-vent length of 25 (male) and 30 mm (female) (Lauck, unpubl. data). The species is widely distributed throughout Tasmania and south-eastern mainland Australia. It breeds in both permanent and ephemeral sites and, in Tasmania, breeding is limited to lentic systems (Littlejohn, 2003). Breeding in the southern forests of Tasmania occurs predominantly in early spring to mid summer and any autumnal breeding seems dependent on rainfall (B. Lauck: pers. obs.). Metamorphosis occurs mostly in January and February. The species is an opportunistic feeder, foraging for litter invertebrates in the terrestrial environment.

The purpose of this study was to document the edge response of *Crinia signifera* at clearcut logging coupe edges in Tasmania, Australia. In spite of the vast number of edge-effect studies, very few have investigated frogs and this is the first study we are aware of to measure edge effects on frogs in Australia. Although *C. signifera* populations are currently considered secure (Cogger, 2000), habitat loss and/or modification is recognised as a threatening process for many frog species and has received little research attention within Australia (Hazell, 2003). Furthermore, data collection for common species is important (Mahoney, 1996) because (1) population declines may be gradual (and, hence, may go unnoticed) and (2) baseline data are required in order to identify any declines that do occur. Hence, understanding the effects of forest management and fragmentation on *C. signifera* populations would augment our understanding of how this species uses modified landscapes.

Methods

Study area

The study area was located within and near the Warra Long Term Ecological Research (LTER) site. The Warra LTER site is located within the southern forests of Tasmania, approximately 60 km south of Hobart and has an elevation range of 37-1260 m (Brown et al., 2001). The specific aims of the Warra LTER site centre on developing an understanding of ecological processes in Tasmania's wet *Eucalyptus obliqua* forests, and on the demonstration and development of sustainable forest management practices (www.warra.com). The forest habitats within and adjacent to three recently harvested coupes (Table 1) were sampled.

Table 1. Characteristics of the sites

Site	Location	Elevation	Landform	Coupe size	Regenerated
Picton	43° 7' S 146° 42' E	150 m	Permian sedimentary	95 ha	2000
Warra	43° 3' S 146° 42' E	400 m	Jurassic dolerite	160 ha	1998
Manuka	43° 6' S 146° 41' E	200 m	Jurassic dolerite	16 ha	1999

In Tasmania's commercial wet eucalypt forests, coupes averaging 50 hectares in size are harvested on a nominal 90-year rotation period (Hickey and Neyland, 2000; Hickey et al., 2001). A high intensity regeneration burn and aerial sowing of eucalypt seed follow clearfell logging. A firebreak, with an approximate width of 10-15 m, is

cleared along the inner edge of coupe boundaries to protect adjacent unlogged forest from post-logging regeneration burns (Westphalen, 2003).

Fieldwork

Transects of pitfall traps were established with the aim of investigating edge and riparian effects on forest litter beetles. Pitfall traps also trapped sufficient numbers of adult *C. signifera* to enable investigation of the edge response of this species.

Because the study was designed as an invertebrate study no ethics approval was required or sought from the Tasmanian Animal Ethics Committee. Although bycatch of a small number of frogs was considered a possibility, the use of lids above the traps was anticipated to prevent this, and the relatively large number of frogs caught was totally unexpected. Rather than waste these animals we decided to use them as the basis of this study.

At each of the three study sites (Table 1), three transects of pitfall traps (318 traps in 45 transects) were randomly located within each of the following habitats:

regeneration forest/logging coupe interior (99 m long transects with traps at 1 m, 5 m, 10 m, 25 m, 50 m, 100 m from a random starting point);

mature forest interior - non-riparian (99 m long transects with traps at 1 m, 5 m, 10 m, 25 m, 50 m, 100 m from a random starting point);

mature forest interior - riparian (99 m long transects with traps at 1 m, 5 m, 10 m, 25 m, 50 m, 100 m from a first order perennial stream);

non-riparian coupe edge (110 m long transects with traps at 5 m and 10 m from the coupe edge into the coupe/firebreak and 1 m, 5 m, 10 m, 25 m, 50 m, 100 m from edge into unlogged mature forest); and

streamside reserve coupe edge (35–105 m variable length transects; traps at 5 m and 10 m into the coupe/firebreak and 1 m, 5 m, 10 m, 25 m, and 50 m (Picton and Warra sites) from both the coupe edge and stream-bank in mature forest; the number of traps per transect (8–11) varied depending on the distance from coupe edge to stream; where applicable, a single trap was used to represent both a distance from the edge and from the stream).

The regeneration forest and mature forest interior transects were randomly located with respect to distance from the forest edge, so particular distances were not replicated. To simplify analyses all forest interior traps were designated as 150 m from the edge.

Pitfall traps were operated for three four-week trapping periods: in winter (June–July 2001), spring (October–November 2001) and summer-autumn (February–March 2002). These periods were spaced four months apart over a twelve-month period in order to account for seasonality. The pitfall traps consisted of 225 mL plastic cups suspended in PVC downpipe sleeves (7.5 cm external diameter, 10 cm deep). The cups were filled to 4 cm depth with ethylene glycol (antifreeze) as a preservative. A 12-cm diameter plastic lid was suspended approximately 3 cm above each trap with three wooden sticks to protect the traps from rainfall and disturbance by vertebrate animals.

Specimens were transferred to 75% ethanol upon return to the laboratory. Snout-vent length (SVL) was measured using callipers (± 0.05 mm) and sex was determined (males have grey and females have white colouring on the ventral surface of the chin – method accurate to within 90% for frogs greater than 20 mm SVL (Lauck, unpubl.

data)). Frogs less than 20 mm SVL were classed as juveniles as this method of sex determination was not reliable for these size classes.

Analyses

To account for unequal sampling of coupe and forest interior relative to each distance along edge transects, results were converted to the number of frogs collected per trap at each distance from the edge.

Mean capture rate with distance was plotted. Non-linear regression (SPSS 10.0 for Windows) was used to determine the relationship between abundance and distance from the edge. The logging coupe interior data point was not included in the non-linear regression because it's pattern was not related to other points rendering the regression meaningless.

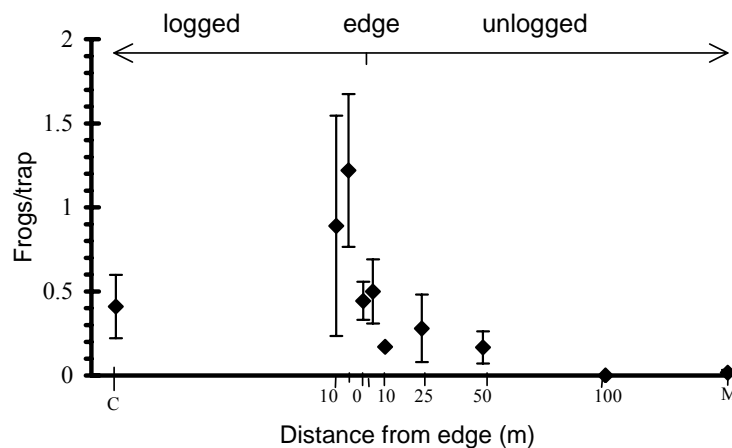
Results

In total, 90 individuals were captured. Of these 7 were male, 29 were female and 54 were juvenile. The relatively low pitfall trap catches in this study are probably related to the trap design chosen for the target study group, which was litter-dwelling Coleoptera. Sixty per cent of captures were in summer-autumn, 37% in spring and only 3% in winter. Eighty-one per cent of summer-autumn and 30% of spring captures were juvenile, whereas all three frogs trapped in winter were adults.

The number of frogs detected in the riparian areas in the streamside reserve edge or unlogged riparian transects was low. Of 16 frogs trapped in streamside reserve transects, the closest they were recorded to a stream was 33-35 m (10 m from the

forest edge in the firebreak). Only one frog was trapped in unlogged riparian transects, 10 m from the stream at Manuka. Since there was no evidence of a riparian response, data from streamside reserve and non-riparian transects were combined for each distance from the forest edge to improve the sample size. Plotting mean \pm SE of frogs/trap with distance (Fig. 1) showed that frog abundance was greatest within the coupe firebreak adjacent to the edge and decreased curvilinearly with distance into the mature forest.

Fig. 1. Abundance (\pm SE) of *C. signifera* across logging coupe edges. ‘C’ indicates coupe interior and ‘M’ unlogged interior forest.



Non-linear regression

Distance from the forest edge explained 31% of the variation in the number of frogs per trap ($F_{1,25} = 11.0540$, $P = 0.0027$). The equation of the line was: frogs/trap = $2.985 - 0.003425(\text{dist}+200)^e$. *Crinia signifera* numbers declined exponentially with distance into unlogged forest and reached an asymptote of negligible abundance 100 m from the edge. Edge penetration by *C. signifera* is estimated to generally fall between 50 m and 100 m.

Discussion

Our results suggest fewer frogs occurred in unlogged interior forest habitat and an elevated abundance occurred in the forest edge/firebreak. *Crinia signifera* was most commonly trapped within the coupe firebreaks, within 10 m of the forest edge.

Abundance decreased exponentially from the edge to negligible levels 100 m within the mature forest interior. Abundance was lower 100 m and beyond into the mature forest than the equivalent distance in the logged coupe. Since *C. signifera* is a disturbance-tolerant species (Margules et al., 1995; pers. comm. F. Lemckert cited in Kavanagh and Webb, 1998), our results are not entirely surprising, but emphasise the importance of sampling both sides of edges rather than only within uncut forest.

We were able to discount food availability as a likely influence of abundance across the edge because beetle abundance (the most significant component of *C. signifera* diet at the site (Lauck, unpubl. data)) was not elevated at the firebreak relative to the forest interior at the study sites (Baker, unpubl. data).

Variations in humidity and ground surface temperatures are also unlikely to explain patterns of *C. signifera* abundance across the edge. Westphalen (2003) recorded edge penetrations of less than 10 m for temperature and humidity at nearby clearfelled logging coupe edges at Warra. Although mean differences in temperatures and humidity were found to be minimal, extremes were greater within logged coupes (Westphalen, 2003). Since the activity patterns of amphibians are thought to decrease with decreasing humidity and increasing temperature (as a result of increased risk of dehydration, Bellis, 1962), amphibians should prefer the more buffered conditions within the forest interior if they were responding to these types of microclimate

determinants. Furthermore, the moisture and microclimatic conditions in logged Tasmanian wet eucalypt forest are probably less restrictive to frogs than in drier climates where frogs are more likely to be constrained to moist refuges.

Availability of standing water rather than forest successional age *per se* is likely a primary factor that may influence the distribution of *C. signifera* across edges. Lauck (2005a), for instance, found that in the same study area, the total amount of standing water within the logged forest was almost twice than the unlogged forest. The incidence of small, ephemeral standing water is greater within the firebreak (and to a lesser extent within the logged coupe) when compared to the forest interior because of the soil compaction caused by heavy machinery during logging and firebreak construction. The value of smaller bodies of standing water as amphibian breeding sites is highly dependent on their hydroperiod. Because the duration of the *C. signifera* larval period can be as short as one month (Williamson and Bull, 1992; Lemckert, 2001), the species is able to utilise relatively small water bodies as successful breeding sites. Tadpoles of *C. signifera* were commonly observed in poorly drained areas both at the forest edge/firebreak and within logging coupe interiors (B. Lauck, personal observation); although it must be noted that even though Lauck (2005a) found a greater abundance of standing water in logged compared to unlogged forest, the amount of standing water used for breeding did not differ significantly between logging treatments. Temporarily flooded areas may be advantageous to tadpole survival due to reduced predation by aquatic predators (Littlejohn, 2003) but it must also be noted, that we did not collect data on the emergence of metamorphs from these smaller ephemeral water bodies and cannot confirm whether metamorphosis was successful or if the ephemeral water bodies acted as ecological traps because they dried before metamorphosis (DiMauro and

Hunter, 2002). Despite this, the creation of fire-dams at intervals along some firebreaks would also provide additional perennial breeding habitat that is less prone to desiccation during dry periods or as the stand ages and this may also explain the high proportion of juveniles captured.

In contrast, poorly drained areas were extremely uncommon within the mature forest stands studied. Water uptake and transpiration by the trees is presumably sufficient to maintain the water table below the soil surface. Although boggy areas do occur within unlogged forest, especially along river flats associated with the larger rivers, the majority of slope forests appear to be generally well drained, with surface water restricted to drainage lines and streams, and natural standing surface water uncommon (S. Baker, personal observation; Lauck 2005a). In our study, riparian areas adjacent to first order perennial streams appeared to be unfavourable habitat for *C. signifera*, presumably because *C. signifera* requires standing rather than flowing water for breeding (Littlejohn and Martin, 1974).

Juveniles were overwhelmingly more common in our samples, constituting half of all captures. It is probable that larger adult frogs were more able to evade capture in the small pitfall traps that were designed specifically for trapping beetles. These data may also be a response to the proximity of breeding sites (see above). Not surprisingly, the majority of juveniles were captured in autumn after the peak period of metamorphosis. Adult captures were greatest during spring coinciding with the period of migration to ponds before breeding. The low capture rate during winter concurs with other findings (Lauck, 2005b) showing activity for this species to be minimal during this period.

Interestingly, adult captures were strongly female biased with only 19% of adult captures male. Behavioural characteristics of male and female *C. signifera* diverge significantly, with males spending extended periods calling at breeding sites whilst females visit for only short periods (Mac Nally, 1983; Lemckert and Shine, 1993). It is unlikely, however, that seasonal differences in activity are responsible for such a female-biased capture, because our sampling periods covered both the peak breeding period in October-November as well as two time periods outside the breeding period in June-July and February-March. Furthermore, pitfall trapping data *within* logging coupes undertaken in the same study area (Bashford et al., 2001; Hickey et al., 2001) demonstrated an even sex ratio for the species (Lauck, 2005b). The female-biased capture in this study may be a reflection of activity patterns that vary with sex because pitfall traps measure the activity density of animals rather than their actual abundance within a habitat (Greenslade, 1964; Melbourne, 1999). For example, females may have a much larger home range and foraging mobility and, thus, may be more likely to encounter pitfall traps. Animal mobility and behaviour (and therefore, pitfall trapability) can also be affected by habitat structure (Greenslade, 1964; Melbourne, 1999); thus an alternative explanation for *C. signifera*'s edge response could be differing mobility in response to habitat conditions. The pitfall trap design employed in this study was developed for invertebrate sampling and while these small pitfalls appeared to effectively trap *C. signifera*, larger traps with drift fences (e.g. Friend et al., 1989) would be preferable in vertebrate studies.

This study was unable to distinguish between effects of firebreak creation and the abutment of two successional habitats. Edge effects vary with edge contrast (Blaustein et al., 1994; Tyler, 1994; deMaynadier and Hunter, 1995) and time since edge creation (Kapos et al., 1997), and the response of *C. signifera* in this study may

be specific to early successional regeneration, where evapotranspiration is likely to be limited because vegetation is still becoming established and surface soil structure remains compacted. Alternative explanations for elevated numbers of *C. signifera* in firebreak traps may be that this species prefers open habitats or attempted to use pitfall traps as refuges where shelter was less available. Removal of logging debris and surface soil results in open habitat with reduced plant growth in the firebreak compared to the logging coupe and mature forest interiors (Westphalen, 2003).

The process of habitat modification appears not to be negatively affecting *C. signifera* within the commercial forests of southern Tasmania. The species' habitat appears to be enhanced by current clearfell logging practices, especially as it seems to be affiliated with the edges produced between different successional stages of harvested forest. These results should not be extrapolated to other species (especially those having very different life history traits), however, because the edge responses of frog species in other studies have been found to be variable (e.g. Gascon, 1993; deMaynadier and Hunter, 1998; Schlaepfer and Gavin, 2001; Toral et al., 2002) and *C. signifera* may be unusually disturbance tolerant. Quantification of ecological responses such as edge effects for declining frog species in Australia is needed to assist wildlife managers in planning for amphibian conservation.

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