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Short-term responses of ground-active beetles to alternative silvicultural systems in the Warra Silvicultural Systems Trial, Tasmania, Australia

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ABSTRACT

The Warra Silvicultural Systems Trial (SST) in Tasmania, Australia provides a framework for investigating the responses of beetles (Order: Coleoptera) to three alternative systems in lowland wet eucalypt forest: aggregated retention; dispersed retention; and understorey islands retained in clearfelled areas. Beetles from three families known to be sensitive to forest management, the families Carabidae (ground-beetles), Curculionidae (weevils) and Leiodidae (fungus-beetles), were collected with pitfall traps prior to harvest, and in the first and third years post-harvest. The retained aggregates in the aggregated retention system maintained beetle assemblages reasonably typical of mature forests, at least in these early years following harvesting. These aggregates appear to provide a stable habitat, with similar species composition in the first and third years post-harvest. In contrast, the harvested areas of the aggregated retention system contained low numbers of beetle species affiliated with mature forest, as did the understorey islands and the dispersed retention system. Relative to clearfelling, all alternative silvicultural systems appeared to be of some benefit to beetles affiliated with mature forest, but aggregated retention retained far greater numbers of these beetles compared to the other systems in Tasmanian wet eucalypt forest.

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1. Introduction

Clearfelling is a widespread silvicultural practice that has long been viewed by the forestry profession as a safe and efficient way of harvesting and regenerating many forest ecosystems in the southern temperate, northern temperate and boreal zones (Lindenmayer and Franklin, 2002; Forestry Tasmania, 2004). However, the social and ecological shortcomings of clearfelling are becoming increasingly apparent (Lindenmayer and Franklin, 1997; Rosenvald and Löhms, 2008) and many members of the Tasmanian public consider that clearfelling is less acceptable than other silvicultural systems (Tasmanian Public Land Use Commission, 1996; Ford et al., 2005). In many parts of the world, the search for appropriate alternatives is converging on the concept of variable retention (Franklin et al., 1997), also known as green-tree retention (GTR) (Vanha-Majamaa and Jalonen, 2001), which is now widely applied in Canada, the Pacific Northwest of the USA and Fennoscandia (Vanha-Majamaa and Jalonen, 2001; Beese et al., 2003; Work et al., 2003; Bunnell and Dunsworth, 2004; Gandhi

et al., 2004; Rosenvald and Löhms, 2008). This approach retains elements of the pre-harvest forest as mature forest habitat embedded in the harvested area (Franklin et al., 1997; Fries et al., 1997; Spence, 2001; Beese et al., 2003). Findings from tests of a range of retention-based silvicultural alternatives suggest that their adoption can bring many benefits for biodiversity, although the benefits vary by region, by silvicultural system and by taxonomic and functional group (Rosenvald and Löhms, 2008).

Clearfell, burn and sow (CBS), on 80–100 year rotations, has been the standard silvicultural system applied in Tasmanian lowland wet eucalypt forest, in which *Eucalyptus obliqua* L'Hérit. and *E. regnans* F.Muell. are the commercially and ecologically dominant tree species (Forestry Tasmania, 1998; Hickey et al., 2006). Because of social and ecological concerns, Forestry Tasmania is committed to reducing clearfelling to no more than 20% of the annual oldgrowth harvest on state forest by 2010 (Forestry Tasmania, 2008). In lowland wet forests, partial harvesting and shelterwood systems are considered both ecologically and economically inappropriate (Nyvold et al., 2005; Hickey et al., 2006). Hence, there is a clear need to develop a more appropriate alternative to CBS in this forest type to help meet this target. The Warra Silvicultural Systems Trial (SST) was established in 1997 to inform Forestry Tasmania about potential alternatives to CBS (Hickey et al., 2001). The choice of a practical alternative was to be guided by economic, safety, social acceptability and silvicultural

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Table 1

Treatments sampled for beetles in the Warra Silvicultural systems trial.

System name and acronym	Description
Clearfell, burn, and sow (CBS)	Large openings with no structural retention, high intensity burn, applied seed
CBS with understorey islands (CBS + UI)	As for CBS but with 40 m × 20 m machinery exclusion zones in up to 5% of the coupe area
Dispersed retention (DRN)	10–15% basal area retention of overstorey eucalypts, low intensity burn, natural seedfall
Aggregated retention (ARN)	30% of coupe area retained in aggregates (AGG) of 0.5–1 ha with the majority of the harvested area (ARN-har) within one tree height of retained forest, low-intensity burn, natural seedfall

practicalities as well as by the ability of the systems to maintain ('lifeboating': [Rosenvald and Löhmus, 2008](#)) and/or rapidly regain species and habitats typical of mature forest that would otherwise be simplified by repeated cycles of CBS ([Hickey et al., 2006](#)).

The individual silvicultural systems in the SST were applied to different coupes (harvest units) each of 11–26 ha ([Table 1](#), [Fig. 1](#)). Each system had different objectives, including expected biodiversity outcomes. Understorey islands (UI) are 0.08 ha (20 m × 40 m) patches embedded within otherwise typical CBS coupes, from which harvesting machinery was excluded in order to provide on-going habitat for coppice-regenerating understorey plant species ([Ough, 2001](#); [Hickey et al., 2006](#)). Mature trees that would otherwise have been felled were often retained in UI in addition to the understorey. The dispersed retention (DRN) system aimed to retain 10% of the pre-harvest basal area of mature trees scattered across the coupe, to provide a natural seed source, to maintain mycorrhizae, to act as habitat trees (e.g., for hollow-dependent fauna) and to provide a steady supply of coarse woody debris in future decades. The aggregated retention (ARN) system aimed to combine the silvicultural advantages of CBS with retention of more robust patches ('aggregates', AGG) of mature forest, each 0.5–1 ha in extent, within the harvested area (ARN-har). These AGG were intended to provide undisturbed habitat for a variety of biodiversity elements, both as long-term refuges in their own right and as a local source of recolonisation of the regenerating harvested area. Regeneration burns were applied to the harvested areas of these systems. Burning of harvesting debris is an important component of Tasmanian wet forest silviculture, sterilising soils and producing an ashbed suitable for seedling germination ([Pryor, 1960](#); [Chambers and Attiwill, 1994](#)).

This paper presents the results of an ongoing study of ground-active beetles (Order: Coleoptera) in a series of coupes that comprise the SST. This is an excellent group with which to explore the response of arthropods to forest management practices. Beetles are an extremely rich component of terrestrial biodiversity, comprising an estimated one fifth of described terrestrial species

([Grove and Stork, 2000](#)), and currently about a third of all species recorded at the Warra Long Term Ecological Research (LTER) site (Forestry Tasmania, unpublished data), in which the SST is embedded. Beetle species vary in dispersal ability, trophic position, habitat requirements, and sensitivity to forest management ([Lawrence and Britton, 1994](#); [Spence et al., 1996](#); [Driscoll and Weir, 2005](#); [Pearce and Vernier, 2006](#); [Driscoll, 2008](#)). Thus, beetles are considered suitable, and are widely used, as ecological indicators ([Ruzicka and Bohac, 1994](#); [Michaels, 1999](#); [Langor and Spence, 2006](#); [Pearce and Vernier, 2006](#)). Recent research has demonstrated that the majority of Tasmanian lowland wet eucalypt forest ground-active beetle species not only have strong preferences for either young regeneration or mature forest, but that approximately half of the species affiliated with mature forest were also found to be sensitive to edge effects ([Baker et al., 2007](#)).

Beetles respond positively to alternative silvicultural systems in northern hemisphere temperate and boreal zones, although responses have varied between studies and silvicultural systems ([Koivula, 2002](#); [Siira-Pietikäinen et al., 2003](#); [Lemieux and Lindgren, 2004](#); [Hyvärinen et al., 2005](#); [Matveinen-Huju et al., 2006](#)). Like the Warra SST, these studies provide an indication of early responses to harvesting, whereas in some cases the main benefits may be expressed over the longer term ([Jacobs et al., 2007](#)). Harvesting intensity (proportion of stand volume removed) can be an important determinant of responses to harvesting treatments ([Koivula, 2002](#); [Siira-Pietikäinen et al., 2003](#); [Hyvärinen et al., 2005](#)). The sensitivity of Tasmanian ground-active beetles to clearfelling, forest age and edge effects ([Michaels and McQuillan, 1995](#); [Baker, 2006a](#); [Baker et al., 2007](#)) allows us to predict that they will respond positively to alternative silvicultural systems that retain mature forest habitat within harvested areas.

Our study focuses on the beetle families Carabidae, Curculionidae and Leiodidae, all of which include many ground-active species. The Carabidae (ground-beetles) are a predatory group, in which approximately one third of the wet eucalypt forest species are flightless. Ground-beetles have a long history of use in bioindication ([Greenslade, 1964](#); [Refseth, 1980](#); [Niemi, 2001](#);

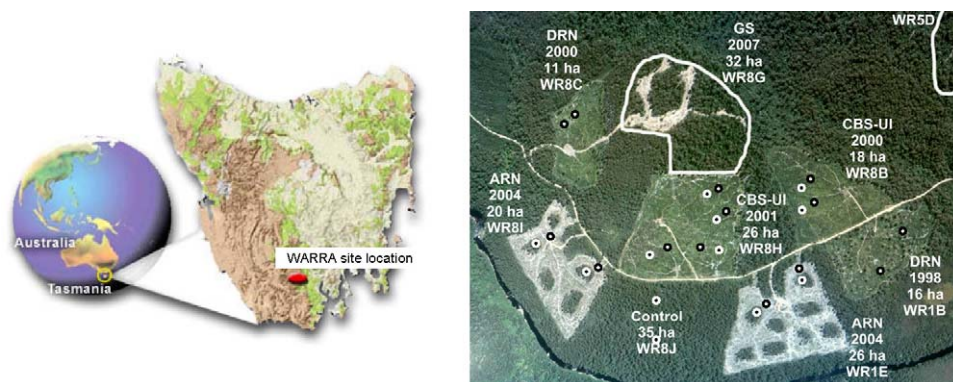


Fig. 1. Location of the Warra LTER site in Tasmania, and locations of beetle collection plots within the Warra Silvicultural Systems Trial. For each coupe, the treatment code, year of regeneration burn, area and coupe name are shown. Black circles with white borders indicate plots in unharvested areas (UI, AGG, CON) and white circles with black borders indicate plots in harvested areas (CBS, DRN, ARN-har).

Niemelä et al., 2007). The Curculionidae (weevils) occupy a different trophic position from the ground-beetles, being primarily phytophagous, phloeophagous or xylophagous (Lawrence and Britton, 1994). The Leiodidae (fungus-beetles) occupy a different trophic position again, being largely mycophagous or scavengers (Lawrence and Britton, 1994). While Curculionidae and Leiodidae are rarely used as indicators elsewhere (but see Chandler and Peck, 1992; Ohsawa, 2005; Zeran et al., 2007), we have previously demonstrated that they are highly responsive to forest management activities in Tasmanian wet eucalypt forest (Baker et al., 2007). Indeed, Jacobs et al. (2007) postulated that fungus-feeding beetles may be more sensitive to harvesting than other trophic groups.

The primary objective of this study was to determine the impacts, compared to CBS, of our three alternative silvicultural systems on ground-active beetles affiliated with mature forest. Overall, we seek to inform future forest management practices aimed at conserving forest biodiversity. Based on sizes of unharvested patches, and their proximity to harvested areas, we hypothesised that, following harvesting, the activity-abundance of beetles affiliated with mature forest would be proportional to the amount of original uncut forest retained within the coupes. We also hypothesised that there would be a time-since-harvesting effect evident in the pattern of similarities and differences in assemblage composition with harvesting treatment.

2. Methods

2.1. Study area

The Warra SST (Fig. 1) is located within the Warra Long Term Ecological Research site (see Brown et al., 2001) at 43.1°S × 146.7°E. It is described in detail in the Introduction and in Hickey et al. (2001, 2006). The harvesting systems are illustrated in more detail in Nyvold et al. (2005). The study area had not been harvested prior to establishment of the SST. The vegetation of unharvested parts of the study area is *E. obliqua* wet forest with either a wet sclerophyll understorey or a thamnic rainforest understorey (see Neyland, 2001 for details). These vegetation types relate to previous fire history, with wet sclerophyll understoreys occurring in areas with a higher fire frequency.

We collected beetles in pitfall traps, in a range of coupes that were later subjected to different silvicultural systems (two coupes per harvesting system: CBS-UI, DRN, ARN), as well as in a coupe that was set aside as a long-term unharvested mature forest control (CON) (Table 1, Fig. 1). In CBS-UI coupes we sampled both the harvested area (CBS) and the understorey islands (UI), and in the ARN coupes we sampled both the harvested area (ARN-har) and the aggregates (AGG).

All the DRN, ARN and CON coupes had wet sclerophyll understoreys, while both the CBS-UI coupes contained areas of wet sclerophyll understorey on the lower slopes and thamnic rainforest understorey on the steeper upper slopes (Neyland, 2001).

Harvesting and burning occurred between 1998 and 2004 (Figure 1, Hickey et al., 2001, 2006). The UI were not given any special protection from the high-intensity regeneration burn typical for CBS, and most (but not all) ended up severely scorched. We assume the harvested area of the CBS-UI coupes to be equivalent habitat for ground-active beetles to CBS coupes without UI, and hence use CBS as a benchmark for comparing other treatments. The post-harvest regeneration burns for DRN were intended to be relatively low-intensity. In practice, some of the retained trees in DRN were burnt in the regeneration burn and many were windthrown over the subsequent few years (Neyland, 2004c). Regeneration burns for ARN-har were experimental and were of a low intensity, but even so, fire encroached into some of

the AGG. The CBS-UI coupes were oversown with eucalypt seed following the regeneration burn, ensuring a dense and rapid regeneration of woody vegetation. The ARN-har and DRN relied on natural seedfall from retained trees and generally experienced slower and more patchy regeneration of woody vegetation.

2.2. Beetle collection and identification

The pitfall trapping program in the SST was described in Bashford et al. (2001). Multiple sample plots of pitfall traps were established in each coupe (total = 26 plots) in the following treatments: CBS and UI; ARN-har and AGG; DRN; and CON. (Table 2, Fig. 1). Plots were located in both harvested and unharvested areas of CBS-UI and ARN coupes. In most coupes, there were two plots of traps in each of the relevant harvested and unharvested habitats (Table 2). Each approximately 20 m × 5 m plot comprised an array of ten pitfall traps forming two rows of five traps, with 5 m between traps and between rows. Previous research has shown that spatial autocorrelation and trap-to-trap interference is unlikely to occur at this trap spacing in this ecosystem (Baker and Barmuta, 2006), in contrast with boreal trapping experience (Digweed et al., 1995). In UI there were sometimes only six pitfall traps per plot because there was not enough space for a larger array; this was corrected for in analysis by using average numbers of beetles per trap. Some plots were not sampled over all allocated sample periods, and thus 68 plot-years were included in our analysis (Table 2).

Plots were sampled prior to harvesting and then the same sampling protocol was repeated in the first and third years post-harvest (referred to as Year-1 and Year-3). This supports examination of not only the immediate effects of harvest but also the trajectory of faunal change over time post-harvest. For each coupe, pitfall traps were generally run continuously for one-year periods (Table 2), with monthly collection and re-setting of traps. Of the 68 plot-years, four were sampled for only eleven months and two plots for only 10 months pre-harvest. Collection periods varied among coupes dependent on the timing of harvesting and regeneration (Table 2). The CON plots were not sampled concurrently with all treatments, but data from a single year each of three years of sampling were used to represent pre-harvest and Year-1 and Year-3 post-harvest for comparisons with harvest treatments.

Once pitfall samples were returned to the laboratory, invertebrates were sieved from the ethylene glycol, and samples stored in 75% ethanol. Beetles were later removed from the samples under a dissecting microscope. For each sample, the abundance and species richness of beetles from all families were recorded. However, identification of beetles to species or morphospecies is very time-consuming. Preliminary analysis indicated that by identifying only the families Carabidae, Curculionidae and Leiodidae we could distinguish CON and CBS plots with equal or greater resolution than if all beetle families were included. Thus we adopted these families as 'indicator families'. The Staphylinidae, although responsive to forest age and harvesting (Gandhi et al., 2004; Baker, 2006a; Buddle et al., 2006; Pohl et al., 2007), were not included because their identification is unduly time-consuming. Focus on this subset of three indicator families approximately halved the laboratory identification time.

Indicator family beetles were dry-mounted, and identified to species or morphospecies using published keys and descriptions (listed in Appendix A) and the Tasmanian Forest Insect Collection (TFIC) housed at Forestry Tasmania. While some morphospecies could only be identified reliably to genus, subfamily or family level, for convenience we use the term species to refer to both described species and morphospecies. By species, 48% were identified to species-level, 33% to genus and 19% to family, subfamily or tribe. All dry-mounted beetles were incorporated into the TFIC.

Table 2

Timing of beetle sampling in the Warra Silvicultural Systems Trial. Plots were sampled for a full twelve months except where indicated with an asterisk (*). Numbers in parentheses after dates are the number of plots.

System	System acronym	Coupe	Habitat	Habitat acronym	Dates		
					Pre-harvest	Year-1	Year-3
Clearfelling with understorey islands	CBS-UI	WR008H	Harvested	CBS	*December 1999–October 2000 (3) *January 2000–October 2000 (1)	August 2001–July 2002 (4)	September 2004–August 2005 (4)
Clearfelling with understorey islands	CBS-UI	WR008H	Understorey Is	UI	November 1999–October 2000 (2) *December 1999–October 2000 (1) *January 2000–October 2000 (1)	August 2001–July 2002 (4)	September 2004–August 2005 (4)
Clearfelling with understorey islands	CBS-UI	WR008B	Harvested	CBS	na	January 2002–December 2002 (2)	September 2004–August 2005 (2)
Clearfelling with understorey islands	CBS-UI	WR008B	Understorey Is	UI	na	January 2002–December 2002 (2)	September 2004–August 2005 (2)
Dispersed retention	DRN	WR008C		DRN	November 1998–October 1999 (2)	September 2001–August 2002 (2)	September 2004–August 2005 (2)
Dispersed retention	DRN	WR001B		DRN	na	November 1998–October 1999 (2)	October 2002–September 2003 (2)
Aggregated retention	ARN	WR008I	Harvested	ARN-har	na	September 2004–August 2005 (2)	October 2006–September 2007 (2)
Aggregated retention	ARN	WR008I	Aggregates	AGG	November 2000–October 2001 (2)	September 2004–August 2005 (2)	October 2006–September 2007 (2)
Aggregated retention	ARN	WR001E	Harvested	ARN har	November 2000–October 2001 (1)	September 2004–August 2005 (2)	October 2006–September 2007 (2)
Aggregated retention	ARN	WR001E	Aggregates	AGG	November 2000–October 2001 (1)	September 2004–August 2005 (2)	October 2006–September 2007 (2)
Control	CON	WR008J		CON	November 1998–October 1999 (2)	September 2004–August 2005 (2)	October 2006–September 2007 (2)

Identification and databasing of all beetles were thoroughly checked prior to analysis, and we are confident that morphospecies were distinguished with a high degree of accuracy.

2.3. Analyses

To correct for unequal numbers of pitfall traps in the arrays in different plots, we used the average number of beetles (activity-abundance) per trap for each plot for each sampling period in analyses. Hence, plot-years ($n = 68$) were the primary sampling unit used in analyses.

One-way analysis of variance using the linear model procedure in R Version 2.7.2 tested whether the trap catches and species richness of beetles at Year-3 post-harvest differed between harvested and unharvested habitats in the silvicultural treatments. Plot averages were used based on the dataset of all beetle families rather than indicator families. We used a one-way ANOVA model, treating plots from replicate sites as independent replicates, to maximise the power for detecting treatment differences in light of limited replication in our experimental design.

We used PC-ORD (McCune and Mefford, 1999) to conduct a non-metric multidimensional scaling (NMS) ordination of beetles in different silvicultural treatments in the three sampling periods based on data for the average trap catches of beetles in plots over each of the three sampling periods. We used the Sorensen distance measure and the program's 'slow and thorough autopilot' mode. To aid interpretation, pre-harvest data from subsequently harvested coupes were used in conjunction with those from CON to provide a larger pool of unharvested mature forest plots. We then used PC-ORD to conduct multi-response permutation procedures (MRPP) to test the statistical significance of pairwise treatment comparisons, based on Year-3 post-harvest assemblage composition data. We used the Euclidean distance measure, and followed the recommendations of Moran (2003) in electing not to conduct Bonferroni

correction of P -values, instead choosing to interpret these conservatively.

We conducted an indicator species analysis (ISA: Dufrêne and Legendre, 1997) in PC-ORD to identify significant indicators of mature unharvested forest and of young regenerating forest post-CBS, in order to allow interpretation of single-species responses to the various silvicultural systems. The analysis was run with 9999 permutations and used pre-harvest data from all treatments (16 plots) and Year-3 post-harvest data from CBS (6 plots).

3. Results

A dataset of 19,239 beetles from 142 species was available for analysis (Appendix B). Of these beetles, 12,009 from 43 species were ground-beetles, 3004 from 29 species were weevils and 4226 from 70 species were fungus-beetles. ANOVA found no evidence to suggest that either the trap catches ($F_{5,20} = 0.6959$, $P = 0.6327$) or species richness ($F_{5,20} = 0.8352$, $P = 0.5401$) of beetles (all families) differed between habitats sampled in the silvicultural treatments at Year-3.

3.1. Assemblage composition

Data were examined to assess whether the limitations of the study design – with low levels of treatment replication and with different coupes having been sampled over different time periods – were likely to bias interpretation of results. Although having only one mature forest CON coupe is an obvious limitation, pre-harvest data from subsequently harvested coupes clustered strongly with CON data from the three sampling years (Fig. 2).

The beetle assemblage composition in unharvested mature forest was relatively consistent across the SST, based on the tight cluster of pre-harvest plots in Fig. 2. Plots within a coupe tended to be closely located in ordination space, and overall geographical

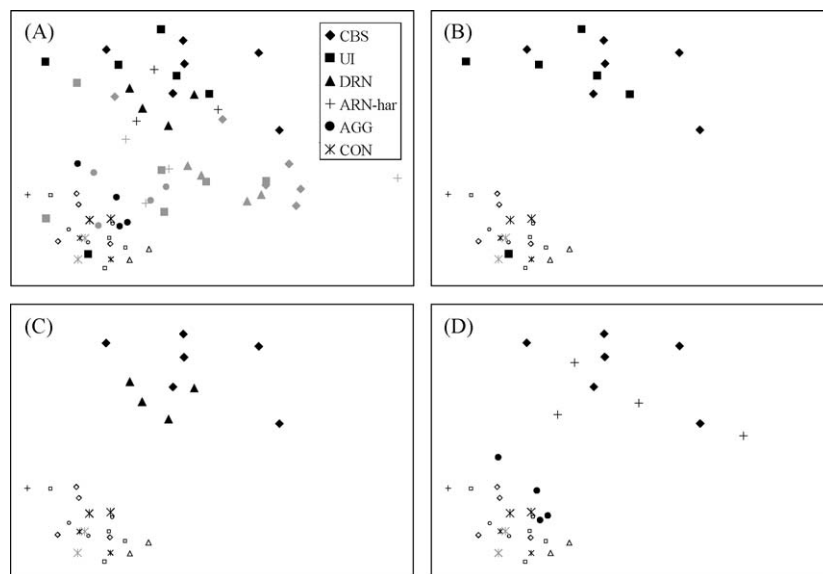


Fig. 2. Non-metric Multidimensional Scaling ordination of beetle assemblages in relation to silvicultural system and time since harvesting, in the Warra Silvicultural Systems Trial, Tasmania. Stress = 15.0% and Instability = 0.00001 after 65 iterations. Plot A illustrates plots in all harvesting systems and the three sampling periods. Plots B–D show a subsample of points to illustrate individual harvesting systems at Year-3 compared to clearfelled and unharvested plots. Plot B illustrates the understory islands, Plot C dispersed retention and Plot D aggregated retention. Small, black, open symbols represent pre-harvest data. Large, grey, closed symbols represent Year-1 post-harvest. Large, black, closed symbols represent Year-3 post-harvest.

separation of sites, and differences in understory vegetation, did not seem to strongly influence beetle assemblage composition. Lack of a full year's worth of pre-harvest data for some plots should not limit interpretation of the analyses since these plots fell within the cluster of other pre-harvest plots in the ordination. Comparisons also indicated that there was relatively little inter-annual variation in beetle assemblage composition in CON plots (Fig. 2). Hence, we considered it valid to use time-since-harvest alone in comparing among areas that had been harvested in different years.

Beetles responded both to silvicultural system and to time-since-harvest (Fig. 2). As previously noted, the CON coupe and pre-harvest data from the harvested sites formed a tight cluster towards the bottom left of the ordination, while beetle assemblage composition clearly changed greatly following harvesting. MRPP found CON to be significantly different from all other treatments at Year-3 post-harvesting ($P < 0.05$; Table 3).

Fig. 2A indicates that except for beetles in AGG, time-since-harvesting (Year-1 versus Year-3) is a strong determinant of assemblage composition. Aggregate plots from both Year-1 and Year-3 are clustered together in a location overlapping with both pre-harvest and Year-1 post-harvest plot locations for the other harvesting treatments. This suggests that AGG provided a stable

habitat for beetles over this time period. Other treatments form scattered clusters relating to time-since-harvesting, with assemblage composition diverging further from that of unharvested forest between Year-1 and Year-3. Within the scattering of plots relating to time-since-harvesting, clustering is also apparent relating to the different harvesting treatments. However, UI, DRN and ARN-har appear to be more similar to CBS in Year-3 than in Year-1. The response to each harvesting treatment is shown, based on Year-3 data, in comparison to beetle assemblages in both unharvested and CBS habitats (Fig. 2B, C and D).

Fig. 2B illustrates the response of beetles in CBS–UI. Plots from four of the six UI fell within the cluster of CBS plots from the same coupes, while one plot was located outside of this cluster but nearby. By contrast, one plot was located within the main cluster of unharvested plots. This latter plot was located within the only UI not to have been burned in the regeneration burn (Neyland, 2004a,b). Despite this outlier, overall assemblage composition in UI did not differ significantly from CBS in MRPP analysis (Table 3).

Fig. 2C illustrates beetle assemblages after DRN. The four plots from the two DRN coupes form a tight cluster close to the scatter of plots from CBS. The cluster of DRN plots overlaps that of CBS (and does not differ significantly in MRPP analysis: Table 3), but is shifted

Table 3
Results of MRPP pairwise comparisons of the assemblage composition of beetles three years after harvest in each silvicultural system in the Warra Silvicultural Systems Trial, Tasmania.

	Clearfelling	Understorey islands	Dispersed retention	Aggregated retention - harvested	Aggregates
Understorey islands	$P = 0.6316$ $A = -0.0078$				
Dispersed retention	$P = 0.4524$ $A = -0.0002$	$P = 0.2366$ $A = 0.0110$			
Aggregated retention - harvested	$P = 0.7180$ $A = -0.0419$	$P = 0.5720$ $A = -0.0079$	$P = 0.1496$ $A = 0.0222$		
Aggregates	$P = 0.0017$ $A = 0.1177$	$P = 0.0037$ $A = 0.0697$	$P = 0.0084$ $A = 0.2032$	$P = 0.0069$ $A = 0.0901$	
Unharvested control	$P = 0.0088$ $A = 0.1297$	$P = 0.0178$ $A = 0.0735$	$P = 0.0187$ $A = 0.3174$	$P = 0.0376$ $A = 0.0987$	$P = 0.0417$ $A = 0.1286$

slightly in the direction of the unharvested plots in the ordination. This suggests that while beetle assemblages in DRN are overall much more similar to CBS than to unharvested plots, their assemblages are a little more similar to unharvested forest than those in CBS.

Beetle response to ARN is illustrated in Fig. 2D. Plots from the ARN separate into two distinct clusters: AGG plots are located very close to unharvested plots, while plots in ARN-har overlap in position with CBS. Beetle assemblages in AGG differed significantly from both CON and all other harvesting treatments ($P < 0.05$, Table 3), including ARN-har. By contrast, ARN-har did not have significantly different assemblage composition from CBS (MRPP: Table 3). However, like DRN, ARN-har appears to support beetle assemblages slightly more similar to unharvested forest than many CBS areas, although there is overlap in the scatter of plots. These analyses suggest that AGG and ARN-har represent two distinct habitats for ground-active beetles in ARN coupes.

Overlaying a joint plot of species vectors with the ordination (not presented) suggested that two fungus-beetles (*Colenisia* TFIC sp 01 and *Zeadolopus* TFIC sp 02), and two ground-beetles (*Homethes elegans* Newman and *Scopodes sigillatus* Germar), all with known habitat preferences for young forest, were correlated in the direction of CBS, DRN and ARN-har plots. These species were all less common in ARN-har than CBS or DRN plots. *S. sigillatus* was most common in DRN plots. Vectors for known mature-forest

species would not be expected to distinguish CBS from ARN-har and DRN plots, because they were all in the direction of CON plots towards the bottom of the ordination. This will be explored further (below) at the level of individual species.

None of the MRPP pairwise comparisons between CBS, UI, DRN and ARN-har showed any significant differences (Table 3). Hence, the CBS, DRN and ARN silvicultural systems result in similar beetle assemblage composition to each other (considering ARN-har rather than AGG which have distinctly different beetle assemblages). However, as previously noted, there is a trend for DRN and ARN-har to have assemblage composition a little more similar to control areas compared to CBS.

3.2. Individual species responses

The majority of species had a strong preference for either young or mature forest, and this influenced their responses to the alternative systems (Appendix B). The indicator species analysis identified 14 significant indicators ($P < 0.05$) of young regeneration and 19 significant indicators of mature forest (Appendix B). Included within these lists of indicators were several of the species considered as indicators of young regeneration or mature forest (edge-tolerant or edge-avoiding) by Baker (2006a, 2006b) and by Baker et al. (2007). Of the 19,239 beetles, the ground-beetles

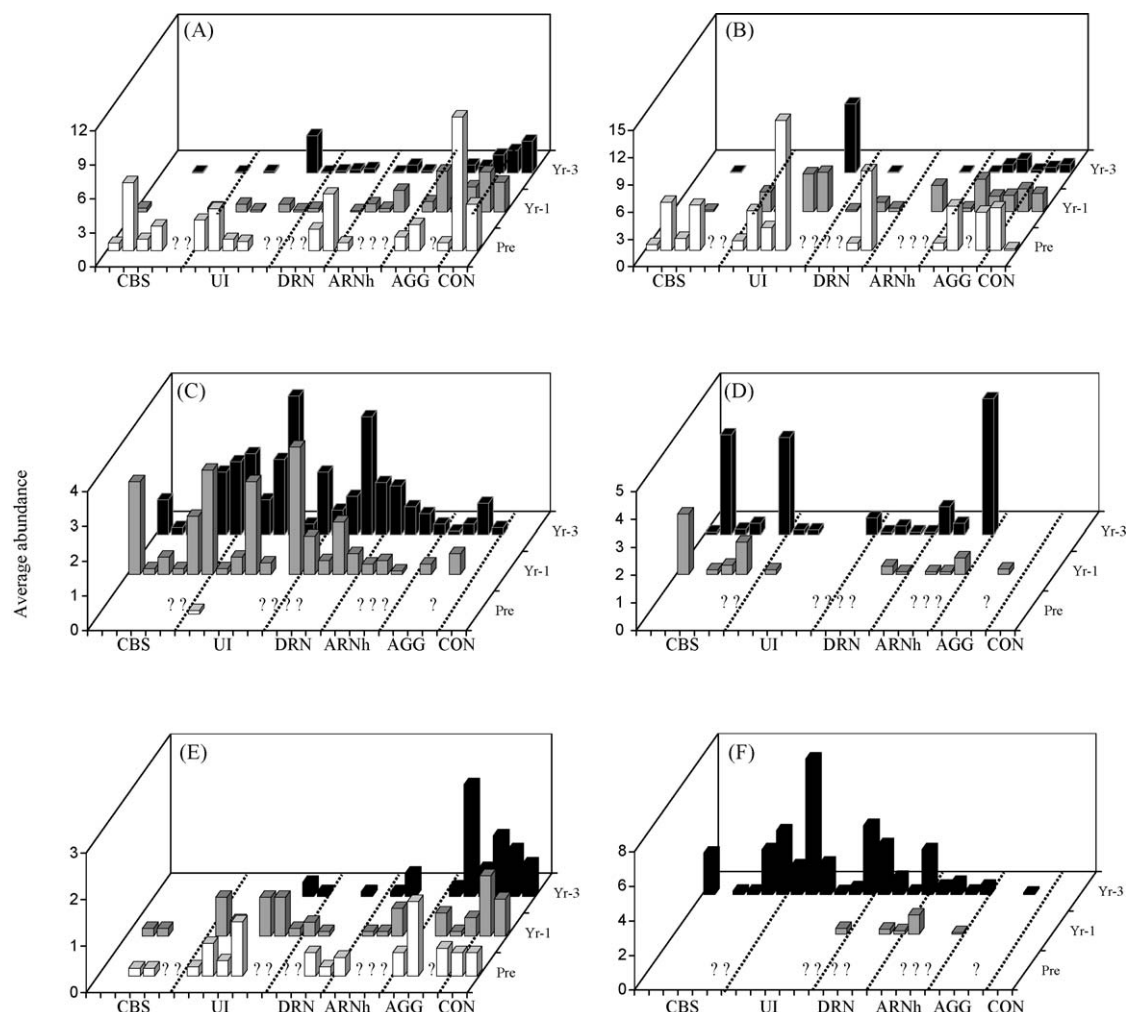


Fig. 3. Activity-abundances of individual beetle species showing contrasting responses to the silvicultural systems in the Warra Silvicultural Systems Trial, Tasmania. Average plot abundances are shown for the three sampling years. A: *Decilaus striatus* is a mature forest edge-avoider. B: *Austronemadus* TFIC sp 03 is a mature forest edge generalist. C: *Scopodes sigillatus* and D: *Cyphotrechodes gibbipennis* are affiliated with young forest. E: *Decilaus* TFIC sp 01 (mature forest) and F: *Colenisia* TFIC sp 01 (young forest) change in activity-abundance between Year-1 and Year-3. Question marks denote pre-harvest plots for which no data were available.

Mecyclothorax ambiguus (Erichson) (6076) and *Notonomus politulus* (Chaudoir) (1974) were the most commonly collected. These species were affiliated with young regeneration and mature forest respectively. Thirty-three species were collected only once, nine species only twice, and 70 species at least ten times.

As a general rule, species affiliated with mature forest were also present in AGG, and in the single unburnt UI. Such species were usually either absent, or had very low levels of activity-abundance, in the harvested areas of all silvicultural systems, and in the five burnt UI. Species affiliated with young forest had the opposite patterns of habitat use. The alternative silvicultural systems were somewhat intermediate between CBS and CON. For example, low numbers of some species affiliated with young forest were collected in AGG, and the trap catches of species indicative of mature forest were often greater in the alternative systems than in clearfelling. However, individual species responses varied greatly (Appendix B).

We use six species to illustrate differing responses to the silvicultural treatments (Fig. 3). The weevil *Decilaus striatus* Lea (Fig. 3A) is a mature forest edge-avoider (*sensu* Baker et al., 2007). In Year-3, this species was present in AGG, but in lower numbers than in CON. It was also collected in relatively high numbers in the unburnt UI. While the species was very rare in CBS and in burnt UI, it had detectable but low levels of activity-abundance in DRN and in ARN-har. The fungus-beetle *Austronemadus* TFIC sp 03 (Fig. 3B) is considered a mature forest edge generalist (*sensu* Baker et al., 2007). It was collected in similar numbers in AGG as in CON, and also had high trap catches in the unburnt UI. It was almost absent from harvested areas and from burnt UI. The ground-beetle *S. sigillatus* (Fig. 3C), a young-forest affiliate, was almost absent from pre-harvest and CON plots, but in Year-3 was collected in all harvesting treatments, including in moderate numbers in AGG. *Cyphotrechodes gibbipennis* (Blackburn) (Fig. 3D) is another ground-beetle affiliated with young forest, but this species appears to be more specific to harvested and burnt areas, and was not detected in AGG nor in the unburnt UI.

The trap catches of some beetle species affiliated with mature forest decreased in harvested areas between Year-1 and Year-3 (Appendix B). For example, *Decilaus* TFIC sp 01 (Fig. 3E) was present in CON and AGG in all three years, but at reduced trap catches in harvested areas and UI in Year-3 relative to Year-1. By contrast, some beetles affiliated with young forest were more common in Year-3 than in Year-1 (Appendix B). For example, the fungus-beetle *Colenisia* TFIC sp 01 (Fig. 3F) was not detected in pre-harvest and CON plots, was only occasionally detected in harvested areas in Year-1, yet was commonly detected in harvested areas and in burnt UI at Year-3. Beetles affiliated with mature forest appeared to undergo lesser changes in trap catches between Year-1 and Year-3, which would account for the stability of AGG in ordination space while the harvested areas shifted position (Fig. 2A). All species collected in the alternative silvicultural systems were also collected in either CBS or CON (Appendix B). Although some species may have been slightly more commonly detected in alternative systems, e.g. ARN-har, there was no strong evidence to suggest that these systems provided unique conditions for any beetles that would not typically be present.

4. Discussion

4.1. Assemblage changes

Ground-active beetles clearly respond to alternatives to clearfelling, and their assemblage composition varied both among systems and with time-since-harvesting. AGG maintained very similar beetle assemblages to CON, providing habitat for beetles affiliated with mature forest. Differences in relative activity-abundance of beetles affiliated with mature forest, e.g. lower trap catches of some edge-

avoiders, and the detection of beetles affiliated with young forest, distinguished AGG from CON. Beetle assemblages in AGG did not differ between Year-1 and Year-3 post-harvest. By contrast, in all other harvested areas, beetle assemblages were more similar to CON in Year-1 than in Year-3. Assemblage composition in one unburnt UI was similar to CON, while beetle assemblages in burnt UI could not be distinguished from those in CBS. Non-statistically significant trends suggested that ARN-har and DRN maintained slightly more beetles affiliated with mature forest than did CBS.

This study corroborates our previous findings (Baker, 2006a), and those of Niemelä et al. (1993) in boreal spruce-pine forest, that ground-active beetles have strong species-specific affinities for either mature forest or young regeneration. These preferences appeared stronger than those of beetles in boreal mixed-wood forest (Jacobs et al., 2008), and were strong determinants of species responses to the alternative harvesting systems. While some species were more commonly detected in the alternative systems than in either CON or CBS, they were scarcely ever entirely absent from one or other of these areas. Hence the alternative systems do not appear to create unique habitat conditions for species that do not usually occur in unharvested mature forest or in CBS, but they do alter the balance of opportunities for use by some of these species. Future sampling will assess whether beetles affiliated with mature forest are able to persist in the harvesting treatments, since some species may be transients that are unable to persist in the longer term. The trap catches and species richness of beetles from all families did not differ among habitats in the various silvicultural treatments.

The Warra SST highlights the role of fire in shaping both the post-disturbance habitat and the beetle assemblages capable of living there. While the responses of beetles to CBS, DRN, ARN-har and AGG were consistent within a treatment, responses to UI varied with regeneration burn impact. This result contrasts slightly with the botanical results in the SST (Neyland et al., 2009), in which burn intensity, and subsequent recovery of understorey vegetation, was variable within the burnt UI. Burnt UI were also structurally different from CBS, containing dead or recovering trees (M. Neyland and S. Baker, unpublished data). Because wildfire is the main natural disturbance event leading to regeneration of wet eucalypt forest (Mount, 1979; Hickey et al., 1998), scorching of some retained stands (UI or AGG) may be desirable. This parallels results from other ecosystems in which fire is integral to forest regeneration and subsequent structure of beetle species assemblages (Apigian et al., 2006; Cobb et al., 2007; Toivanen and Kotiaho, 2007). In a study of boreal mixed-wood ground-beetles in Alberta, Canada, Koivula and Spence (2006) found that assemblage composition was strongly influenced by fire severity.

Given the small size of UI, it is surprising that the unburnt UI supported mature forest beetles, including known edge-avoiders. In some cases, trap catches of these species were greater than in unharvested forest. There was also a trend for greater trap catches of some species in AGG than in CON in the year following harvesting. Hence, our study raises the possibility that both AGG and unburnt UI may be used by dispersing mature forest beetles seeking refugia following harvesting. Gandhi et al. (2004) proposed that harvest residuals could act as refugia for adult beetles dispersing from harvested areas. In a study in Canadian lodgepole pine-dominated forest, they found that one species of flightless ground-beetle was caught more often in harvest residuals than in uncut forest, although overall beetle assemblage composition was similar (Gandhi et al., 2004).

In general, mature forest species that were present in reasonable numbers in UI in Year-1, were much less commonly detected, if at all, by Year-3. By contrast, most species in this category that were detected in AGG in Year-1 were able to maintain their activity-abundance in Year-3, and sometimes were able to enhance their trap catches beyond levels found in CON. It may be that species affiliated

with mature forest use all these treatments as refugia but can only breed successfully in the larger patches (i.e. in AGG) because of their greater resilience to edge-effects (MacArthur and Wilson, 1967; Didham et al., 1998). Interestingly, Gandhi et al. (2004) found that shape, but not size, of harvest residuals affected beetle activity-abundance and diversity, with round patches having greater ground-beetle activity-abundances. Other studies have found that fragment area is not necessarily a major influence on mature forest beetles (Davies and Margules, 1998; Gandhi et al., 2001), although small patches are likely to be infiltrated by species affiliated with young forest (Halme and Niemelä, 1993; Spence et al., 1996). Nevertheless, we feel confident that the very small UI are unlikely to provide equivalent habitat for edge-avoiding species (Baker et al., 2007) in the longer term compared to larger AGG.

Post-harvest beetle assemblages of DRN and ARN-har were not significantly different from those of CBS. However, they were slightly offset in ordination space from the main cloud of CBS assemblages in the direction of CON assemblages, suggesting that they were nevertheless subtly different. We can think of two potential explanations for this patterning. The level of retention in DRN and ARN, but not in CBS-UI, may enable the survival in the harvested areas (at least in the short-term) of some beetles belonging to species affiliated with mature forest. Alternatively, the lower intensity and patchier nature of the burns in ARN-har and DRN (M. Neyland, unpublished data) may have produced more fire refugia, such as unburnt logs, than in the high-intensity CBS burn. Beetle assemblages in UI, DRN, and ARN-har became more similar to those in CBS in Year-3 relative to Year-1. It is not clear from our study whether this difference from CBS would persist – or even become more pervasive – beyond the first few years after harvest. Evidence from elsewhere suggests that beetles affiliated with mature forest tend not to persist in young forest regenerating after harvest, even if they are present immediately after harvesting (Niemelä et al., 1993; Pohl et al., 2007). On the other hand, in a study of ground-beetles and GTR in British Columbia, Lemieux and Lindgren (2004) did not detect a distinct mature forest fauna, but nevertheless found that retained patches (0.1–2 ha) exerted a slight influence on the fauna of the harvested areas, largely through influencing one common species.

4.2. Limitations

The study design, with only two treatment replicates and with other sampling limitations, created challenges for analysis and interpretation of a nature that will be familiar to many ecologists (Field et al., 2007). However, to a large degree the large number of beetles sampled (approximately 20,000) and the long-term nature of the study, with pre- and post-harvest data and with low background variability among years and across the study area, minimise the adverse impacts of these shortcomings. The very strong response of beetles to silvicultural system are obvious in spite of these design limitations; however, caution should prevail when extrapolating findings beyond the study area, since responses may differ regionally. Additionally, the results represent only early responses to harvesting within the context of an approximately 80-year silvicultural rotation.

4.3. Implications

The order in which the treatments retained beetles affiliated with mature forest more or less fit our expectations, with (1) AGG and the unburnt UI performing best, followed by (2) ARN-har and DRN, (3) burnt UI, and (4) CBS. From this it appears that the 'aggregated' form of GTR has better prospects for maintaining mature forest beetle biodiversity than the 'dispersed' form. Hence, we predict that the speed of progression along the trajectory of

recovery of beetle assemblages will be faster for ARN-har than for either DRN or CBS (with or without UI), at least initially, because of the presence of mature forest refugia within the harvested area. Whether this translates into long-term differences in assemblage composition in the regenerating stands remains a matter for ongoing research at Warra. In particular, it would be important to determine whether AGG are able to provide a source of individuals to recolonise the harvested area once the regeneration is of a suitable age. In the US Pacific Northwest, aggregated GTR treatments were more effective at retaining mature forest ground-beetle and spider assemblages than were dispersed GTR treatments, although none did so as well as unharvested mature forest (Halaj et al., 2008). Nevertheless, ARN is not guaranteed to maintain beetle biodiversity typical of mature forest. In a Finnish study, Koivula (2002) determined that the small size of the aggregates (comprising 20–30 mature trees) included in the pine silvicultural system that he studied were too small for the continued survival of pre-harvest mature forest ground-beetle assemblages. In another Finnish ground-beetle (and spider) study in spruce forest, Matveinen-Huju et al. (2006) detected similar effects through distinguishing responses of species based on preferences for moist or dry habitat. They found that the prevalence of moisture-loving species declined in aggregates over the three years following harvest, whereas the prevalence of more dry-tolerant species increased, suggesting that the aggregates dry out over time. Thus we cannot exclude the possibility that the AGG in our study will also become less suitable for some beetles over time. However, it is worth noting that the aggregates in the Finnish study were intermediate in size between the UI and AGG in our study, and that the beetle fauna in AGG in our study appeared stable between Year-1 and Year-3 post-harvest. Other studies on edge effects would suggest that at least the larger (>1 ha) AGG would be sufficiently resilient to stand a good chance of retaining mature forest faunas (Baker et al., 2007). Current recommendations for aggregates in operational coupes are that they should generally exceed 1 ha in size (Forestry Tasmania, 2007); thus they may also be more resilient than the smaller aggregates in our study.

Canadian studies comparing beetles in natural fire refuges with those in patches retained during harvesting (Gandhi et al., 2001, 2004) showed that while unharvested patches maintained beetle assemblages similar to those in typical unharvested forest, they differed from those in fire residuals. Fire residuals were older than the surrounding unharvested forest, indicating that careful choice of the location, structure, age and microhabitat of aggregates may influence the degree to which they support beetles equivalent to fire refuge habitat. In Tasmania, guidelines for locating aggregates in operational ARN (Forestry Tasmania, 2007) specify that "aggregates should be anchored on specific locations of ecological value (e.g. biological legacies, special vegetation communities) and include the range of habitat types (e.g. vegetation types, stand ages, landforms) present within the coupe." Therefore, while aggregates may not be exactly equivalent habitat to fire refuges, some areas likely to be skipped by natural fires will tend to be included among a coupe's aggregates.

The unharvested mature forests in the SST area have not been burnt by wildfire since at least 1934 (Hickey et al., 1998), and have not been burnt by stand-replacing wildfire for much longer than this. Hence, unharvested areas have at least a seven-decade 'head start' over the harvested areas on the succession towards rainforest (Gilbert, 1959; Jackson, 1968). We have previously demonstrated a high degree of congruence in the ground-active beetle faunas of Tasmanian lowland wet eucalypt forest three decades following CBS with those of equivalent forest three decades following stand-replacing wildfire (Baker et al., 2004). This situation mirrors their vegetation species compositional similarities at the same stage in their succession (Hickey, 1994; Turner, 2003). Beetles in Tasmania

and elsewhere demonstrate succession in assemblage composition in relation to stand age (Michaels and McQuillan, 1995; Buddle et al., 2006; Paquin, 2008), although Driscoll (2005) found substantial overlap of ground-active beetle communities in Tasmanian wet eucalypt forest and rainforest—two successional stages of very different ages. However, we do not currently know the age at which forest becomes suitable for 'oldgrowth'-dependent beetle species, nor even whether the term 'oldgrowth' has ecological relevance for beetles in this system. Convergence of beetle faunas with pre-disturbance conditions can be quite rapid in some ecosystems (Watts et al., 2008) but not in others (Niemelä et al., 1993; Buddle et al., 2000; Halaj et al., 2008).

Wet eucalypt forest with a rainforest understorey occurs when these forests have been subjected to infrequent fires, while pure rainforest requires an absence of wildfire for several hundred years (Jackson, 1968; Alcorn et al., 2001). On this timescale, an 80-year harvesting cycle is not long. However, it is hoped that in the alternative systems trialled at Warra, the beetle faunas of the harvested areas will more rapidly converge with those of the unharvested parts. It remains to be seen whether this occurs before the next harvesting cycle. A guideline for operational ARN in Tasmanian State forest, that states that "the majority of the felled area should be within one tree height of forest that is retained for at least a full rotation" is intended to ensure 'mature forest influence' over the majority of the harvested area (Forestry Tasmania, 2007). Proximity to mature forest has been shown to be an important factor in seed dispersal of rainforest trees and in their germination in the harvested area (Tabor et al., 2007). Increasing forest influence in ARN relative to CBS is therefore expected to help increase the 'successional age' of the regeneration, from one having primarily sclerophyllous understories to one having greater representation of rainforest species. It is also anticipated that by containing patches of older forest in AGG, that remain unharvested for at least one silvicultural cycle, ARN harvesting can take the forest and its beetles further along the successional trajectory towards rainforest than is possible with CBS. Thus when the surrounding regenerated forest is 80 years old, the AGG will be 80 years older still. If it had been 70 years since the last wildfire at the time of the last harvest, then by the end of the first silvicultural cycle these AGG will not have experienced wildfire for 150 years. Whether AGG will be left unharvested for a second silvicultural cycle will depend on what objectives future generations of managers set for them.

Results from our study more or less concur with those on birds (Lefort and Grove, in this issue) and vascular plants (Neyland et al., 2009) that were run concurrently in the SST area. Birds, plants and ground-active beetles operate on different spatial and temporal scales, yet all groups seem to fare better under ARN compared to DRN or CBS-UI. This gives us confidence in stating that expanding ARN into the production forest landscape in place of some CBS – as is now envisaged on State forest in Tasmania (Forestry Tasmania, 2007, 2008) – is likely to provide some general biodiversity benefits for species that inhabit mature forest.

The high degree of sensitivity of ground-active beetles to harvesting systems, and the fact that they represent approximately one third of species recorded at Warra, demonstrates the value of including these invertebrates as a monitoring taxon despite their identification being relatively time-consuming compared to birds or vascular plants. The 'indicator family' approach taken with this study, where only the Carabidae, Leiodidae and Curculionidae were identified, gave excellent results while approximately halving the laboratory time of a more taxonomically encompassing study. A mixture of these three families probably better represents the total ground-active beetle fauna than just a single beetle family (such as the widely used Carabidae) since it incorporates a greater range of responses and habitat affinities.

In Europe, many beetle species – particularly those associated with oldgrowth or mature forest – have become threatened as a result of intensive forestry activities (Niemelä, 1997; Jonsson and Kruys, 2001). By contrast, in Tasmania, native forest harvesting is currently usually still occurring in areas with little or no previous harvesting, and very few species are yet recognised as being under threat. Nevertheless, the European experience argues strongly for developing forest management practices in Tasmania that are better able to maintain mature forest beetle assemblages within production forestry landscapes. Tasmanian beetles have also been shown to be sensitive to fragmentation, with some flightless species showing a negative relationship with patch isolation (Driscoll, 2008). Ground-active beetles, like other taxa that have relatively poor dispersal abilities, are therefore likely to benefit from 'lifeboating', enabling continuous occupation of stands (Rosenvald and Lohmus, 2008). Hence, alternative silvicultural systems, in particular aggregated retention, appear to have good scope in helping to maintain populations of sensitive beetle species within the production forestry matrix.

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Appendix A

List of references consulted in the identification of beetle taxa appearing in this study.

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[illegible]

Species	n	Pre-harvest						Year-1 post-harvest					
		CBS	UI	DRN	ARN-har	AGG	CON	CBS	UI	DRN	ARN-har	AGG	CON
<i>Amblystomus nigrinus</i>	121	0	0	0	0	0	0	0.78	0.11	0.05	0.25	0.03	0
<i>Amblytelus striatus</i>	3	0	0	0	0	0	0	0.06	0.03	0	0	0	0
<i>Anomotarus illawarrae</i>	4	0	0	0	0	0	0	0	0	0	0	0	0
<i>Carabidae</i> TFIC sp 12	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Chylinus ater</i> (M)	499	0.46	0.49	1.80	0.10	1.40	2.90	0.31	0.56	0.83	0.63	1.30	1.70
<i>Clivina</i> TFIC sp 01	10	0	0	0	0	0	0	0	0	0	0.10	0	0
<i>Cyphotrechodes gibbipennis</i> (Y*)	193	0	0	0	0	0	0	0.64	0.03	0.10	0.20	0.05	0
<i>Diaphoromerus</i> TFIC sp 01	13	0	0	0	0	0	0	0.06	0.03	0	0.03	0.03	0
<i>Dystrichothorax tasmaniensis</i>	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Euthenarus nigellus</i> (Y)	79	0	0	0	0	0	0	0	0	0	0.25	0.03	0
<i>Euthenarus promptus</i>	10	0	0	0	0	0	0	0	0	0.03	0.05	0	0
<i>Homethes elegans</i> (Y*)	127	0	0	0	0	0	0	0.22	0.08	0.43	0.05	0.03	0
<i>Homethes sericeus</i>	1	0	0	0	0	0	0	0	0	0.03	0	0	0
<i>Homethes</i> TFIC sp 01	5	0	0	0	0	0	0	0	0	0.03	0.08	0	0
<i>Hypharpax australasiae</i>	43	0	0	0	0	0	0	0.25	0	0.05	0.05	0.03	0
<i>Hypharpax moestus</i>	120	0	0	0	0	0	0	0.19	0.06	0.03	0.03	0.05	0
<i>Hypharpax peroni</i>	1	0	0	0	0	0	0	0.03	0	0	0	0	0
<i>Lestignathus cursor</i>	5	0	0	0.05	0	0	0	0	0	0.10	0	0	0
<i>Lestignathus pieperi</i>	1	0.04	0	0	0	0	0	0	0	0	0	0	0
<i>Mecyclothorax ambiguus</i> (Y*)	6076	0	0.03	0	0	0	0	32.14	11.1	23.33	58.85	4.13	0.05
<i>Notagonum marginellum</i>	34	0	0	0	0	0.03	0	0.61	0	0.10	0.18	0	0
<i>Notonomus politulus</i> (M)	1974	2.92	3.88	13.30	2.40	2.70	3.00	4.50	5.31	8.75	3.10	2.78	2.05
<i>Pentagonica vittipennis</i>	3	0	0	0	0	0	0	0.06	0.03	0	0	0	0
<i>Pericompso australis</i>	20	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pseudoceneus sollicitus</i> (Y)	419	0	0	0	0.10	0	0	0.89	0.03	0	7.08	0.03	0
<i>Pterocyrtyus globosus</i>	1	0	0	0.05	0	0	0	0	0	0	0	0	0
<i>Pterocyrtyus tasmanicus</i>	4	0	0	0	0	0	0	0	0.11	0	0	0	0
<i>Pterocyrtyus</i> TFIC sp 02	1	0.04	0	0	0	0	0	0	0	0	0	0	0
<i>Rhabdotox reflexus</i> (M)	285	0.17	0.62	1.25	0.60	2.27	1.15	0.17	0.39	0.40	0.18	1.08	0.05
<i>Scopodes boops</i> (Y)	487	0	0	0	0	0	0	3.69	1.06	1.80	1.40	0.15	0
<i>Scopodes griffithi</i>	111	0	0	0	0	0	0	0.06	0	0	2.05	0.03	0
<i>Scopodes sigillatus</i> (Y*)	396	0	0.03	0	0	0	0	1.36	1.22	0.90	0.20	0.23	0
<i>Scopodes tasmanicus</i>	30	0	0	0	0	0	0	0.11	0.03	0.05	0.08	0	0
<i>Simodontus australis</i>	5	0	0	0	0	0.03	0	0	0	0.03	0	0	0
<i>Sloaneana tasmaniae</i>	630	0.38	0.28	1.95	0	0.50	0.95	0.25	1.42	4.65	1.43	0.75	0.65
<i>Stichonotus leai</i>	30	0	0	0.05	0	0.07	0	0.0					

Appendix B (Continued)

Species	n	Pre-harvest						Year-1 post-harvest					
		CBS	UI	DRN	ARN-har	AGG	CON	CBS	UI	DRN	ARN-har	AGG	CON
Cryptorhynchinae TFIC sp 11	2	0	0	0	0	0	0.05	0	0	0	0	0.03	0
Cryptorhynchinae TFIC sp 20	11	0.21	0.13	0	0	0.03	0	0	0	0	0	0	0.05
Cryptorhynchinae TFIC sp 38	1	0	0	0	0	0	0.05	0	0	0	0	0	0
Cryptorhynchinae TFIC sp 45	1	0	0	0	0	0	0	0	0	0	0	0	0.05
Cryptorhynchinae TFIC sp 49	1	0	0	0	0	0.03	0	0	0	0	0	0	0
Curculionidae nr Dryophthorinae TFIC sp 01	1	0	0	0	0	0	0	0	0	0	0	0	0
Curculionidae TFIC sp 39	3	0	0	0.05	0	0	0	0	0	0	0.05	0	0
Curculionidae TFIC sp 40	5	0	0	0	0	0	0	0.03	0	0	0	0.03	0
Curculionidae TFIC sp 41	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Decilaus albonotatus</i>	32	0.08	0.03	0.10	0.20	0.03	0.10	0	0	0	0.10	0.15	0.20
<i>Decilaus lateralis</i> (M,EA*)	149	0.87	1.47	0.65	0	1.00	0.20	0.06	0.14	0.03	0.03	0.15	0.40
<i>Decilaus nigronotatus</i> (M,EA*)	92	0.38	1.04	0.40	0	0.27	0.25	0.03	0.06	0.03	0	0	0.25
<i>Decilaus striatus</i> (M,EA*)	735	2.46	2.06	3.45	0.70	1.40	7.95	0.11	0.28	0.15	0.73	1.98	3.05
<i>Decilaus</i> TFIC sp 01 (M)	204	0.08	0.60	0.35	0.40	0.90	0.50	0.06	0.50	0.10	0.20	0.25	1.05
<i>Decilaus</i> TFIC sp 02 (M)	298	0.33	0.30	0.60	0.40	1.20	1.65	0.03	0.03	0.10	0.50	1.20	1.70
<i>Decilaus</i> TFIC sp 03 (M)	120	0.79	0.40	0.35	0	0.27	0.50	0.03	0.31	0.13	0.10	0.25	0.35
<i>Decilaus</i> TFIC sp 04 (M,EA*)	682	0.88	1.43	1.00	0.10	2.93	5.35	0.06	0.97	0.23	0.95	1.55	2.95
Diabthrariinae TFIC sp 02	1	0	0	0	0	0.03	0	0	0	0	0	0	0
<i>Dinichus terreus</i> (M)	241	0.67	0.23	0.50	2.00	1.10	1.00	0.17	0.39	0.48	0.28	0.63	0.55
<i>Dryophthorus</i> ECZ sp 02	2	0	0	0	0	0	0	0	0	0	0	0.03	0
<i>Emplexis</i> TFIC sp 01	1	0	0	0	0	0	0	0	0	0	0.03	0	0
Entiminae TFIC sp 15	1	0	0	0	0	0	0	0	0	0.03	0	0	0
<i>Exeiratus carinatus</i>	6	0	0.03	0	0	0.03	0	0	0.06	0	0.03	0	0
<i>Exeiratus</i> TFIC sp 01	5	0	0	0	0	0	0.05	0.03	0.03	0	0	0.03	0
<i>Exeiratus</i> TFIC sp 03	53	0	0.03	0	0	0	0	0.03	0.11	0.08	1.03	0.03	0
<i>Exeiratus</i> TFIC sp 04	172	0.08	0.07	0	0	0.47	0	0	1.03	0	0.13	0.03	0
<i>Exeiratus</i> TFIC sp 07 (M)	30	0.33	0.27	0.15	0.10	0	0.15	0	0.06	0.03	0	0	0
<i>Exeiratus</i> TFIC sp 08	5	0	0	0	0.10	0	0	0	0	0	0	0	0
<i>Exithius capucinus</i> (M)	36	0.04	0.13	0.25	0	0.07	0.10	0.03	0.03	0.05	0.05	0.08	0.10
<i>Exithius loculiferus</i>	12	0	0	0	0	0	0	0	0	0.03	0.05	0.03	0.05
<i>Exithius</i> TFIC sp 02	2	0	0	0	0	0	0	0	0.03	0	0	0.03	0
<i>Exithius</i> TFIC sp 03	6	0	0.03	0	0	0	0	0	0.06	0	0	0.05	0
<i>Exithius</i> TFIC sp 05	20	0	0.08	0	0.20	0.07	0.10	0	0	0.03	0.08	0.08	0.05
<i>Exithius</i> TFIC sp 06	10	0	0.03	0.05	0	0.07	0	0	0.06	0.03	0.03	0.03	0
<i>Exithius</i> TFIC sp 07	2	0	0	0	0	0.03	0	0	0	0	0	0	0
<i>Leptopius</i> TFIC sp 01	4	0	0	0	0	0.03	0	0	0.06	0	0	0	0
<i>Mandalotus arciferus</i>	40	0.21	0.25	0	0	0.27	0	0.06	0.22	0.05	0	0	0
<i>Mandalotus blackburni</i>	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Mandalotus muscivorus</i>	297	0.17	0.20	0.35	0.10	0.50	0.30	0.28	0.58	0.50	0.20	0.85	0.20
<i>Mandalotus</i> sp nr <i>vacillans</i>	48	0	0.15	0.10	0	0.33	0.05	0	0	0.03	0.08	0.28	0
<i>Mandalotus</i> TFIC sp 14	1	0	0	0	0	0	0.05	0	0	0	0	0	0
<i>Merimnetes</i> TFIC sp 10	11	0	0	0	0	0	0.15	0.06	0	0	0	0	0.10
<i>Meriphus?</i> TFIC sp 01	3	0	0.08	0	0	0	0	0	0	0	0	0.03	0
<i>Miocallus pygmaeus</i>	3	0	0	0	0	0	0	0	0	0	0	0.03	0
<i>Mylorhinus</i> TFIC sp 03	8	0	0	0	0	0.03	0	0	0.03	0	0.03	0	0
<i>Orthorhinus</i> TFIC sp 01	1	0	0	0	0	0	0	0	0.03	0	0	0	0
<i>Pachyporopterus satyrus</i>	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Platypus subgranosus</i>	3	0	0	0	0	0	0	0	0	0.05	0	0	0
<i>Poropterus alboscuteularis</i>	11	0	0	0.05	0	0	0.05	0.06	0	0.03	0	0.05	0
<i>Poropterus antiquus</i>	12	0.08	0	0	0.10	0	0	0	0.03	0.03	0	0.05	0
<i>Poropterus succisus</i>	7	0	0.03	0	0	0	0	0.03	0	0.03	0	0.03	0
<i>Prostomus murinus</i>	14	0	0	0	0.10	0	0	0	0	0.03	0.03	0.08	0.10
<i>Prypnus scutellaris</i>	1	0	0	0	0	0	0	0	0	0	0	0	0
Rhadinosominae TFIC sp 02	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Rhadinosomus</i> TFIC sp 01	4	0	0	0	0	0	0	0	0	0	0	0	0
<i>Rhamphus acaciae</i>	4	0	0.03	0	0	0	0	0	0.03	0	0.03	0	0
Rhytirhininae TFIC sp 01 (Y)	139	0	0	0	0	0	0	0.39	0.33	1.53	0.35	0.05	0
<i>Roptoperus tasmaniensis</i> (M)	198	0.88	0.64	0.50	0	0.43	1.55	0.08	0.14	0.30	0.23	0.15	1.15
<i>Symbothinus</i> TFIC sp 01	2	0	0	0	0	0	0	0.06	0	0	0	0	0
Tychiinae TFIC sp 01	1	0	0	0	0	0	0	0	0	0	0	0	0
Tychiinae TFIC sp 13	1	0	0	0	0	0	0	0	0	0	0	0.03	0
Tychiinae TFIC sp 30	1	0	0	0	0	0	0	0	0	0	0	0.03	0
Tychiinae TFIC sp 31	2	0	0	0	0	0	0	0	0	0.05	0	0	0
Tychiinae TFIC sp 32	1	0	0	0	0	0	0	0	0.03	0	0	0	0
Tychiinae TFIC sp 33	2	0	0	0	0	0	0	0.03	0.03	0	0	0	0
Tychiinae TFIC sp 34	1	0	0	0	0	0	0	0	0	0.03	0	0	0
<i>Tyrtaeosus ustulatus</i>	3	0	0	0	0.10	0	0	0	0.03	0	0	0	0
Species	n	Year-3 post-harvest											
		CBS	UI	DRN	ARN-har	AGG	CON						
Carabidae													
<i>Acallistus longus</i> (M)	206		0.03		0.11		0.13		0.03		0.45		0.15
<i>Adelotopus dubius dubius</i>	1		0		0		0.03		0		0		0
<i>Agonocheila curtula</i>	1		0		0.02		0		0		0		0

Appendix B (Continued)

Species	n	Year-3 post-harvest					
		CBS	UI	DRN	ARN-har	AGG	CON
<i>Amblystomus nigrinus</i>	121	0.08	0.03	0.10	1.63	0	0
<i>Amblytelus striatus</i>	3	0	0	0	0	0	0
<i>Anomotarus illawarrae</i>	4	0	0.03	0	0.08	0	0
<i>Carabidae</i> TFIC sp 12	1	0	0.03	0	0	0	0
<i>Chylus ater</i> (M)	499	0.15	0.48	0.35	0.13	1.50	2.55
<i>Clivina</i> TFIC sp 01	10	0	0	0.13	0.03	0	0
<i>Cyphotrechodes gibbipennis</i> (Y*)	193	1.30	0.16	0.15	1.58	0	0
<i>Diaphoromerus</i> TFIC sp 01	13	0	0.03	0.08	0.10	0	0
<i>Dystriothorax tasmaniensis</i>	1	0.02	0	0	0	0	0
<i>Euthenarus nigellus</i> (Y)	79	1.12	0	0	0.03	0	0
<i>Euthenarus promptus</i>	10	0.05	0	0	0.10	0	0
<i>Homethes elegans</i> (Y*)	127	0.53	0.66	0.73	0.15	0	0
<i>Homethes sericeus</i>	1	0	0	0	0	0	0
<i>Homethes</i> TFIC sp 01	5	0.02	0	0	0	0	0
<i>Hypharpax australasiae</i>	43	0.02	0.03	0.13	0.55	0	0
<i>Hypharpax moestus</i>	120	0.10	0.25	1.30	0.98	0.03	0
<i>Hypharpax peroni</i>	1	0	0	0	0	0	0
<i>Lestignathus cursor</i>	5	0	0	0	0	0	0
<i>Lestignathus pieperi</i>	1	0	0	0	0	0	0
<i>Mecyclothorax ambiguus</i> (Y*)	6076	6.15	1.62	2.43	13.4	0.08	0
<i>Notagonum marginellum</i>	34	0	0	0	0	0	0
<i>Notonomus politulus</i> (M)	1974	0.32	0.77	1.00	0.38	4.88	4.00
<i>Pentagonica vittipennis</i>	3	0	0	0	0	0	0
<i>Pericompsus australis</i>	20	0	0	0	0.50	0	0
<i>Pseudoceneus sollicitus</i> (Y)	419	0.35	0.03	0.23	1.70	0.03	0
<i>Pterocyrus globosus</i>	1	0	0	0	0	0	0
<i>Pterocyrus tasmanicus</i>	4	0	0	0	0	0	0
<i>Pterocyrus</i> TFIC sp 02	1	0	0	0	0	0	0
<i>Rhabdotes reflexus</i> (M)	285	0.02	0.04	0.10	0.03	1.20	0
<i>Scopodes boops</i> (Y)	487	0.18	1.02	0.43	2.93	0	0
<i>Scopodes griffithi</i>	111	0.30	0	0	0.20	0	0
<i>Scopodes sigillatus</i> (Y*)	396	0.97	1.93	1.68	0.78	0.38	0
<i>Scopodes tasmanicus</i>	30	0.05	0.14	0.18	0.13	0	0
<i>Simodontus australis</i>	5	0	0	0	0	0.08	0
<i>Sloaneana tasmaniae</i>	630	0.87	0.61	1.68	0.23	0.68	0.65
<i>Stichonotus leai</i>	30	0	0.02	0	0	0.03	0.10
<i>Tasmanorites grossus</i>	9	0	0.12	0	0	0	0
<i>Trechimorphus diemenensis</i> (Y)	43	0.10	0.02	0	0.03	0	0
<i>Trechinae</i> TFIC sp 08	4	0	0.03	0	0	0	0
<i>Trechobembix baldiensis</i>	2	0	0.02	0	0	0	0
Leiodidae							
<i>Austronemadus</i> TFIC sp 03 (M,EG)	827	0.02	1.27	0.03	0.03	0.70	0.75
<i>Catoposchema tasmaniae</i> (M)	40	0	0	0.05	0	0.18	0.15
<i>Choleva</i> TFIC sp 01 (M,EA*)	299	0.02	0.17	0.05	0.08	0.53	2.50
<i>Colenisia</i> TFIC sp 01 (Y)	310	1.52	2.65	1.68	0.48	0.03	0
<i>Colon</i> TFIC sp 03	45	0.07	0.06	0.08	0.03	0	0
<i>Colon</i> TFIC sp 04	36	0.12	0	0.03	0.10	0	0
<i>Colon</i> TFIC sp 05 (Y)	119	0.32	0.13	0.05	1.25	0	0
<i>Colon</i> TFIC sp 06	72	0.03	0.14	0.08	0.18	0	0
<i>Colon</i> TFIC sp 08 (Y)	100	0.23	0.37	0.13	0.03	0	0
<i>Colon</i> TFIC sp 09	43	0.13	0.03	0	0.20	0.03	0
<i>Colon</i> TFIC sp 10	23	0.03	0.02	0.10	0.13	0.03	0
<i>Colon</i> TFIC sp 11	3	0	0	0	0	0	0
<i>Colon</i> TFIC sp 12	21	0	0	0	0.05	0	0
<i>Colon</i> TFIC sp 13	1	0	0	0.03	0	0	0
<i>Colon</i> TFIC sp 14 (Y)	50	0.20	0.03	0.08	0.23	0	0
<i>Colon</i> TFIC sp 15	6	0.03	0.04	0	0	0	0
<i>Eublackburniella</i> TFIC sp 01	1	0	0	0	0	0	0
<i>Myrmicholeva acutifrons</i>	1	0	0.03	0	0	0	0
<i>Myrmicholeva ligulata</i>	11	0	0	0	0	0.05	0
<i>Nargiotes gordonii</i>	9	0	0	0	0	0	0
<i>Nargomorphus bryanti</i>	1	0	0	0	0	0	0
<i>Nargomorphus globulus</i>	574	0.95	8.99	0.65	0.08	0.35	0.45
<i>Nargomorphus jeanneli</i>	59	0.05	0.56	0.48	0.03	0.10	0.05
<i>Nargomorphus nitidus</i>	7	0.03	0.03	0.03	0.03	0.03	0.05
<i>Nargomorphus victoriensis</i>	5	0	0	0.03	0	0	0
<i>Neopeltops</i> TFIC sp 01	11	0.02	0.06	0.05	0.08	0.03	0
<i>Sogdini</i> 'ANIC gen B' TFIC sp 01	31	0.10	0.20	0	0	0	0.05
<i>Sogdini</i> SEAGO 'gen nov A' TFIC sp 01	2	0	0.02	0	0	0	0
<i>Zeadolopus</i> TFIC sp 02 (Y*)	297	1.38	1.04	1.10	0.53	0.35	0.40
Curculionidae							
<i>Ancyrtalia oleariae</i>	6	0	0	0	0	0	0.10
<i>Cryptorhynchinae</i> TFIC sp 07 (M)	450	0.02	0.20	0.35	0.30	1.18	2.15
<i>Cryptorhynchinae</i> TFIC sp 10	1	0	0	0	0	0	0

Appendix B (Continued)

Species	n	Year-3 post-harvest					
		CBS	UI	DRN	ARN-har	AGG	CON
Cryptorhynchinae TFIC sp 11	2	0	0	0	0	0	0
Cryptorhynchinae TFIC sp 20	11	0	0	0	0	0	0.05
Cryptorhynchinae TFIC sp 38	1	0	0	0	0	0	0
Cryptorhynchinae TFIC sp 45	1	0	0	0	0	0	0
Cryptorhynchinae TFIC sp 49	1	0	0	0	0	0	0
Curculionidae nr Dryophthorinae TFIC sp 01	1	0	0	0	0	0.03	0
Curculionidae TFIC sp 39	3	0	0	0	0	0	0
Curculionidae TFIC sp 40	5	0	0.02	0	0	0.05	0
Curculionidae TFIC sp 41	1	0	0.02	0	0	0	0
<i>Decilaus albonotatus</i>	32	0	0	0	0.03	0.18	0
<i>Decilaus lateralis</i> (M,EA*)	149	0.02	0.07	0.03	0	0.10	0.30
<i>Decilaus nigronotatus</i> (M,EA*)	92	0	0.19	0.03	0	0	0.20
<i>Decilaus striatus</i> (M,EA*)	735	0.03	0.59	0.23	0.25	0.78	2.40
<i>Decilaus</i> TFIC sp 01 (M)	204	0	0.07	0.03	0.15	1.13	0.85
<i>Decilaus</i> TFIC sp 02 (M)	298	0.08	0.33	0.03	0.15	1.00	0.85
<i>Decilaus</i> TFIC sp 03 (M)	120	0.03	0.05	0.03	0.15	0.15	0.30
<i>Decilaus</i> TFIC sp 04 (M,EA*)	682	0.03	0.51	0.10	0.40	2.48	2.45
Diabathrariinae TFIC sp 02	1	0	0	0	0	0	0
<i>Dinichus terreus</i> (M)	241	0	0.15	0.15	0.28	0.35	0.45
<i>Dryophthorus</i> ECZ sp 02	2	0	0	0.03	0	0	0
<i>Emplexis</i> TFIC sp 01	1	0	0	0	0	0	0
Entiminae TFIC sp 15	1	0	0	0	0	0	0
<i>Exeiratus carinatus</i>	6	0	0	0	0	0.03	0
<i>Exeiratus</i> TFIC sp 01	5	0	0	0	0	0	0.05
<i>Exeiratus</i> TFIC sp 03	53	0.02	0	0	0.03	0	0
<i>Exeiratus</i> TFIC sp 04	172	0.02	1.80	0	0.05	0	0
<i>Exeiratus</i> TFIC sp 07 (M)	30	0	0	0	0.03	0	0.05
<i>Exeiratus</i> TFIC sp 08	5	0	0.03	0	0	0.05	0
<i>Exithius capucinus</i> (M)	36	0	0.04	0.10	0.03	0.08	0.05
<i>Exithius loculiferus</i>	12	0.02	0	0	0.05	0.05	0.10
<i>Exithius</i> TFIC sp 02	2	0	0	0	0	0	0
<i>Exithius</i> TFIC sp 03	6	0	0	0	0	0.03	0
<i>Exithius</i> TFIC sp 05	20	0	0	0	0.03	0.08	0
<i>Exithius</i> TFIC sp 06	10	0	0	0	0	0	0.05
<i>Exithius</i> TFIC sp 07	2	0	0	0	0	0	0.05
<i>Leptopius</i> TFIC sp 01	4	0	0	0	0	0.03	0
<i>Mandalotus arciferus</i>	40	0.03	0.07	0.03	0	0	0
<i>Mandalotus blackburni</i>	1	0	0.02	0	0	0	0
<i>Mandalotus muscivorus</i>	297	0.38	0.81	0.70	0.10	1.48	0.25
<i>Mandalotus</i> sp nr <i>vacillans</i>	48	0.02	0.02	0.05	0.03	0.23	0
<i>Mandalotus</i> TFIC sp 14	1	0	0	0	0	0	0
<i>Merimnetes</i> TFIC sp 10	11	0.07	0	0	0	0	0
<i>Meriphus?</i> TFIC sp 01	3	0	0	0	0	0	0
<i>Miocallus pygmaeus</i>	3	0	0	0	0.03	0	0.05
<i>Mylloporhinus</i> TFIC sp 03	8	0.02	0.05	0	0	0	0.05
<i>Orthorhinus</i> TFIC sp 01	1	0	0	0	0	0	0
<i>Pachyporopterus satyrus</i>	1	0	0	0.03	0	0	0
<i>Platypus subgranosus</i>	3	0	0	0	0	0.03	0
<i>Poropterus alboscuteellaris</i>	11	0.02	0	0	0.03	0.05	0
<i>Poropterus antiquus</i>	12	0	0.08	0.03	0	0.03	0
<i>Poropterus succisus</i>	7	0.02	0.03	0.03	0	0	0
<i>Prostomus murinus</i>	14	0.02	0.06	0	0	0.05	0.05
<i>Prypnum scutellaris</i>	1	0	0	0	0	0.03	0
Rhadinosominae TFIC sp 02	1	0.02	0	0	0	0	0
<i>Rhadinosomus</i> TFIC sp 01	4	0.03	0	0.05	0	0	0
<i>Rhamphus acaciae</i>	4	0	0	0.03	0	0	0
Rhytirhininae TFIC sp 01 (Y)	139	0.22	0.08	0.15	0.35	0	0
<i>Roptoperus tasmaniensis</i> (M)	198	0.05	0.12	0.18	0.25	0.23	0.40
<i>Symbothinus</i> TFIC sp 01	2	0	0	0	0	0	0
Tychiinae TFIC sp 01	1	0.02	0	0	0	0	0
Tychiinae TFIC sp 13	1	0	0	0	0	0	0
Tychiinae TFIC sp 30	1	0	0	0	0	0	0
Tychiinae TFIC sp 31	2	0	0	0	0	0	0
Tychiinae TFIC sp 32	1	0	0	0	0	0	0
Tychiinae TFIC sp 33	2	0	0	0	0	0	0
Tychiinae TFIC sp 34	1	0	0	0	0	0	0
<i>Tyrtaeosus ustulatus</i>	3	0	0.02	0	0	0	0

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