Beetles and fuelwood harvesting: a retrospective study from Tasmania's southern forests

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Abstract

Coarse woody debris (CWD) is a key component of forest ecosystems, ultimately supporting perhaps the majority of forestdependent species. In many parts of the world, forestry practices that diminish CWD have been shown to impact heavily on saproxylic (CWDdependent) species. Plans for wood-fired power stations as a part of integrated wood-processing facilities being developed in Tasmania give cause for concern because it is CWD that will *be harvested as fuelwood. This paper outlines a study undertaken to help understand the* potential impacts of fuelwood harvesting on biodiversity. Two pairs of study sites in the southern forests were sampled for saproxylic beetles in summer 2004/05. All sites supported regenerating forest following harvesting in the 1980s. One member of each pair of sites had been harvested by conventional clearfell, burn and sow (CBS) silviculture, while the other member of each pair had additionally been subjected to fuelwood harvesting (CBS-FW) which resulted in lower levels of retained CWD.

Trends in species richness with treatment were inconsistent, but lowered overall beetle abundance in CBS-FW compared to CBS, and differences in assemblage composition at the coupe level, strongly suggested an impact of fuelwood harvesting over and above that of CBS. In general, trends were clearer among obligately saproxylic species than among facultatively saproxylic species, while nonsaproxylic species either showed a weaker trend, no trend or a trend in the opposite direction to the saproxylic species. These findings agree with the hypothesis that saproxylic species richness and composition are related to the abundance of CWD, but need to be treated with caution given the limited scope of the study. They are perhaps best viewed as supportive evidence available to be combined with findings from related research projects to give guidance as to the likely extent of impacts of future fuelwood harvesting, and ways in which these impacts can be mitigated.

Introduction

In this age of heightened concern over humanity's reliance on fossil fuels and their contribution to climate change, the utilisation of forest biofuels is often portrayed as an environmentally sound practice (Wall 1999; Kraxner et al. 2003). Forest biomass is already a major contributor to the power supplies of some forest-rich countries (e.g. Finland: Hakkila 2006). A wood-fired power station is one of the anticipated components of the integrated wood processing facilities at the Huon Wood Centre in Tasmania's southern forests; an equivalent facility is also anticipated in northwest Tasmania. These power stations, if built, would potentially increase the recovery of logs, including coarse woody debris (CWD), from harvested coupes within their catchments. A review of the science behind industrial fuelwood harvesting in Tasmania (Raison *et al.* 2002) concluded that such power stations could have 'considerable greenhouse benefits'.

However, CWD is also widely recognised as an important habitat for a range of forest species that are collectively termed saproxylic (dead-wood-dependent). Saproxylic species, occurring in a wide range of taxonomic groups, can comprise the majority of forest-dwelling species, not just beetles (Siitonen 2001; Grove 2002a). It is no coincidence that countries with a history of intensive use of forest biofuels are also those with major conservation issues in regards to saproxylic species (e.g. Sweden: Jonsell *et al.* 1998).

Understanding the impact of fuelwood harvesting on saproxylic biodiversity requires multiple approaches. For instance, the future availability of CWD (for harvest or as habitat) can be modelled based on harvesting trials and on CWD surveys; this was one of the main recommendations arising from the review of Raison et al. (2002). It has been assumed, but not demonstrated, that fuelwood harvesting in Tasmania's forests would have an impact on local biodiversity over and above that of harvesting under clearfell, burn and sow (CBS) silviculture (Grove et al. 2002). However, the extent of any potential impact of industrial fuelwood harvesting at the coupe scale cannot be so readily gauged, since impacts in addition to those evident at the time of harvesting may develop in the following decades. There are at least two reasons for this delayed response. One is because CWD decays gradually over time, so while it may appear relative abundant immediately post-harvest this is a temporary phenomenon, assuming no further inputs. Another is because it may take a few years for the population responses of dependent insects to take effect, given their usual generation times of one to several years.

Impacts of fuelwood harvesting following CBS (hereafter referred to as CBS-FW) over the ensuing rotation could take the form of changes in abundance, species richness or assemblage composition relative to CBS without fuelwood harvesting. Species with an obligately saproxylic status (i.e. those that depend entirely upon CWD or other dead wood habitats) may have more difficulty maintaining populations than species with a facultatively saproxylic status (i.e. those that may also be able to utilise leaf litter or fine woody debris). Testing these ideas requires a retrospective study - not an easy proposition if industrial fuelwood harvesting is yet to be introduced to the landscape.

Fortunately (from a research perspective), some limited fuelwood harvesting was conducted in parts of Tasmania's southern forests in the 1970s and 1980s. It occurred at a time when the pulp mill at Port Huon was looking for cheaper sources of fuel as a substitute for oil (R. Evans, Forestry Tasmania, pers. comm.). The demand for fuelwood was relatively small, which meant that in any one year there were some CBS coupes from which fuelwood was harvested and other CBS coupes from which it was not harvested. Although this pattern of use does not help inform the likely impacts of landscape-wide fuelwood harvesting, it has enabled this retrospective study, focusing on paired examples of both types of regenerating coupe.

The specific aim of this study, therefore, is to examine whether limited past fuelwood harvesting led to any discernible local-scale effects on saproxylic beetle assemblages, as a pointer towards understanding any need for management constraints on future, largerscale fuelwood harvesting.

Methods

Site selection

Candidate sites for the study were selected following discussions with Forestry Tasmania Huon District staff. Several criteria were set for selection of study sites from the list of candidate sites. One was that all sites should comprise wet eucalypt forest regeneration following CBS. The hardest criterion to meet was a necessity for each CBS-FW site to be paired with a geographically close CBS site of a similar regeneration age, and with similar aspect. slope and altitude. Additionally, it was required that each CBS-FW site had been subjected to fuelwood harvesting over a sufficiently large area to enable multiple sampling locations at least 50 m from any other treatment. It was also a requirement that fuelwood harvesting had been carried out at a sufficient intensity for a visibly noticeable reduction (compared to the paired CBS site) in the availability of CWD. This last criterion was determined subjectively: no reliable data exist on how much fuelwood was harvested from these coupes, and it is equally uncertain how

the amount removed would compare with future fuelwood harvesting scenarios.

Through adopting these selection criteria, and after field surveys of several additional sites on the shortlist, two pairs of study sites were found, one at a location in the Arve region and the other at a location in the Russell region (Figure 1).

Description of study sites

The two Arve sites comprise a CBS coupe (AR048H) on Arve Road, harvested in 1976, and a CBS-FW coupe (AR050G) on Arve Loop, harvested in 1983. The minimum direct distance between the two areas targeted for sampling in these



Figure 1. Location of the Russell and Arve study sites in Tasmania's southern forests. State forest is shaded pale grey; formal reserves (including those on state forest) are shaded dark grey; the WHA boundary is shown as a hatched line. The two solid black circles denote the clearfell, burn and sow (CBS) study-sites, while the two black-outlined circles denote the additionally fuelwood-harvested (CBS-FW) study-sites.

Table 1. The sites in Tasmania's southern forests used to examine the effects of past fuelwood harvesting on beetles. Locations are georeferenced in decimal degrees. CBS = clearfell, burn and sow without fuelwood harvesting; CBS-FW = clearfell, burn and sow accompanied by fuelwood harvesting.

	Arve CBS	Arve CBS-FW	Russell CBS	Russell CBS-FW
Coupe name	AR048H	AR050G	RU028DN	RU028DS
Coupe location	43.1083 S	43.9020 S	43.1202 S	43.9030 S
	146.7644 E	146.7498 E	146.7812 E	146.7483 E
Altitude	320 m	200 m	430 m	420 m
Year of regeneration	1976	1983	1990	1990

coupes is about 1400 m. The two Russell sites comprise two parts of a single coupe (RU028D), harvested in 1990. The CBS part is to the north of Russell Road that bisects the coupe, while the CBS-FW part is to the south of this road. The minimum direct distance between the two areas of this coupe targeted for sampling is about 300 m. The Russell sites are situated about 22 km to the north of the Arve sites.

Table 1 gives some basic information about these study sites.

Sampling

Sampling focused on beetles, because of their proven value in forest biodiversity studies, particularly those concerning the saproxylic habit (e.g. Grove 2000).

The sampling unit for this study consisted of a Malaise trap, with four pitfall traps each positioned 2-3 m away from its four corners. The Malaise and pitfall traps were of the standard design. Thus, each pitfall trap consisted of a plastic drinking cup (85 mm top diameter) placed into a buried section of PVC pipe so that the rim of the cup was flush with the soil surface. A plastic lid supported by sticks was placed over the cup to exclude rain. Pitfall traps were charged with diluted (c. 10%) ethylene glycol, while the Malaise trap collecting head contained undiluted (c. 95%) ethanol. Additionally, a line of plastic troughs containing diluted ethylene glycol was laid

on the ground along the lower margin of the intercepting netting of the Malaise trap. This was intended to trap flying insects that reacted to hitting the interception netting by dropping downwards rather than heading upwards towards the Malaise trap collecting head.

Four sampling units were established in each study site, making a total of 16 sampling units (i.e. 16 Malaise traps, 16 trough traps and 64 pitfall traps). Units were situated at least 10 m from one another. So as not to bias the samples towards saproxylic species, sample units were deliberately positioned away from large logs, while in order to increase sample size they were positioned in potential insect flight paths (i.e. along shrubfree 'corridors' arising through the natural patchiness of shrub growth). The traps were established in early November 2004. Samples were collected roughly every two weeks from 22 November 2004 until 25 February 2005, when the traps were decommissioned.

'Passive' collecting methods, as used in this study, are considered preferable for sampling the local species pool compared to more targeted methods such as emergence traps or direct examination of dead wood (Alinvi *et al.* 2007). They better reflect the activity levels of species in the general area and hence take into account the relative rarity of the CWD from which those sampled individuals originated. In contrast, more targeted methods reflect relative abundances in the substrate itself, regardless of its overall rarity.

Sorting and analysis

All beetles were removed from the samples: individuals from the first month of collection (November to December 2004) were mounted, labelled, identified and recorded in the Forestry Tasmania biodiversity database in accordance with standard protocols in place for the Tasmanian Forest Insect Collection (TFIC) at Forestry Tasmania, Hobart. The rest of the samples remain unsorted, but the entire collection resides in the TFIC. Samples from the four pitfall traps in each sampling unit were merged prior to sorting, but the Malaise trap collecting-head sample and Malaise trap trough sample from each sampling unit were kept separate from each other and from the merged pitfall sample. For the level of analysis presented in this paper, data from all concurrent samples within a sampling unit were merged. Sitelevel summary data presented in this paper are based on merging all four sampling units at a site, but sampling units were kept separate for more complex analyses.

Not all species could be formally identified; taxa for which only partial identification was possible were allocated morphospecies names consistent with those of other specimens of the same taxon in the TFIC. For convenience, both formally identified species and morphospecies are hereafter referred to simply as species. Species were categorised as either saproxylic or nonsaproxylic, and saproxylic species were further categorised as either facultative or obligate. These classifications were based on a developing understanding of beetle ecology from a range of recent studies in the southern forests, particularly Grove et al. (2008), Yee (2005) and Yee et al. (2001).

Choice of statistical analyses was constrained by the low level of betweentreatment and within-site replication in the study design - itself a reflection of the difficulty of finding suitable study sites. Summary univariate statistics (species richness and abundance) are therefore presented in tabular form without further statistical analysis. Since the assemblage structure comprised many rare species and rather few common species, multivariate analyses aimed at comparing assemblage composition were conducted on squareroot-transformed abundance data. to reduce the relative influence of the commonest species, and the Brav-Curtis distance measure was used. Species with a total abundance of one across all samples ('singletons') were removed from all datasets used for multivariate analyses. Nonmetric multidimensional scaling (NMS), an unconstrained ordination technique, was conducted using the 'slow and thorough auto-pilot' routine in PC-ORD (McCune and Mefford 1999) to identify any patterns in the beetle assemblage composition data consistent with site or treatment effects. Canonical analyses of principal coordinates (CAP), a constrained ordination technique, were run in the program CAP (Anderson and Willis 2003), to test more formally the hypotheses of no site and treatment effects (in separate analyses). One feature of CAP is a 'leave-one-out' analysis. This gives an indication of the robustness of the program's separation of the data into predetermined groups (i.e. sites or treatments), by re-running it numerous times, each time without one of the rows of data (plot replicates), and seeing what proportion of these runs is able to correctly classify the data into the predetermined groups. The lower the proportion of 'leave-one-out' analyses that have misclassification errors, the more robust the distinction among those groups. CAP allows the presentation of ordination plots similar to those presented in this paper for NMS. However, for the purposes of this study, it was felt sufficient to present the summary statistics only.

Having the same low number (2) of treatment replicates as site replicates enabled the compilation of a third dataset, comprising what were termed 'false treatment' data; these were also run through CAP. This data-set was configured

Table 2. Numbers of individuals and species of beetles sampled, based on a range of data-sets derived from two pairs of study sites in Tasmania's southern forests. CBS = clearfell, burn and sow without fuelwood harvesting; CBS-FW = clearfell, burn and sow accompanied by fuelwood harvesting.

		Arve CBS	Arve CBS-FW	Russell CBS	Russell CBS-FW	Combined CBS	Combined CBS-FW	Total
All beetle species	Individuals	5260	4767	3900	3431	9160	8198	17358
	Species	191	171	170	175	246	238	317
Non-saproxylic	Individuals	1130	667	603	862	1732	1529	3261
species	Species	33	40	35	38	49	58	74
Saproxylic	Individuals	4131	4100	3297	2569	7428	6669	14097
species	Species	158	131	135	137	197	180	243
Facultatively saproxylic species	Individuals Species	3292 89	3482 70	2711 66	1938 71	6003 102	5420 93	11423 121
Obligately saproxylic species	Individuals Species	839 69	618 61	586 69	631 66	1425 95	1249 87	2674 122

to test whether it was still possible to obtain significant differences from what were no more than artificially constructed 'treatments'. For this purpose, the Arve CBS plots were lumped with the Russell CBS-FW plots and presented to the program as one 'false treatment', to be compared with another 'false treatment' made from a lumping of the Arve CBS-FW and the Russell CBS plots. For all CAP analyses, 9999 permutations of the original data were used.

Results

The beetle fauna

The data-set comprised 17,358 individual beetles of 317 species, representing 61 beetle families (Appendix 1; Table 2). Of these 317 species, 159 could be identified to named species, with the remaining 158 referable to morphospecies only. A single individual of the threatened, saproxylic Mount Mangana stag-beetle *Lissotes menalcas* was collected, in the Arve CBS site. The conservation status of all other species remains undetermined although none are listed as threatened. Eighty-one per cent of all collected beetle individuals were considered to be saproxylic. Of these, 81% of individuals belonged to species categorised as facultatively saproxylic, while the remaining 19% of individuals belonged to obligately saproxylic species. A breakdown by species revealed a somewhat different pattern, with 77% of species being saproxylic, of which 50% of species were facultatively saproxylic and 50% were obligately saproxylic. Facultatively saproxylic beetle species tended to be represented by many more individuals compared to the situation with obligately saproxylic beetle species, while non-saproxylic species tended to be represented by the fewest individuals (Figure 2). Eighty-five species were represented as singletons only (and hence were excluded from multivariate analyses), while, at the other end of the abundance spectrum, six species were each represented by over a thousand individuals. This very uneven distribution of individuals among species necessitated the square-root-transformation of abundance data in multivariate analyses, as discussed above.

Abundance and species richness comparisons between treatments

Table 2 shows the numbers of individuals and species for CBS and CBS-FW sites separately, based on a range of subsets of the entire data-set. For all saproxylic datasets, there were fewer individuals sampled in CBS-FW compared to CBS (for example, 6669 compared to 7428 overall), although the absolute differences were often small and neither individual site showed this effect consistently across all sub-groups of saproxylic species. For the non-saproxylic data-sets, there were more individuals sampled in CBS-FW compared to CBS at Russell but considerably fewer at Arve. Species richness differences were also inconsistent. While overall species richness was lower in CBS-FW compared to CBS in all the saproxylic data-sets considered (and 180 compared to 197 overall), the absolute differences were often small. For Arve, all comparisons involving saproxylic data-sets indicate a lower species richness in CBS-FW compared to CBS. For Russell, there were more facultatively saproxylic species but fewer obligately saproxylic species. For the non-saproxylic beetles data-set, species richness was higher in CBS-FW compared to CBS at both sites (and 58 compared to 49 overall).

Assemblage composition

Figure 3 shows ordination plots based on the two most informative axes of what were either two- or three-dimensional solutions to the non-metric multi-dimensional scaling ordinations performed on each of the five data-sets shown in Table 2. Some separation between sites and/or treatments is evident for every data-set, indicating that different sites and different treatments support different beetle assemblages. Separation is most apparent in the larger data-sets (all beetles, and all saproxylic beetles). The least evidence of separation is shown by



Figure 2. Rank abundance curves, each based on one of three components of the entire data-set of beetles derived from four study sites in Tasmania's southern forests used to examine the effects of past fuelwood harvesting on beetles. The three components are facultatively saproxylic, obligately saproxylic and non-saproxylic beetle species.



Figure 3. Ordination plots of assemblages of beetles based on separate non-metric multidimensional scaling analyses of five beetle data-sets (lettered a to e) derived from four study sites in Tasmania's southern forests used to examine the effects of past fuelwood harvesting on beetles. The data-sets were square-root transformed and had all singletons removed; the Bray-Curtis (Sorensen) distance measure was used. The same symbols are used to represent the same sites and treatments in each chart. CBS stands for clearfell, burn and sow; CBS-FW stands for clearfell, burn and sow accompanied by fuelwood harvesting.

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the non-saproxylic beetles (which comprise the smallest data-set). Generally, locations show more consistent separation than do treatments (sites) at each location, but these are sometimes confounded. For instance, the facultatively saproxylic beetle species data-set shows a clear separation by treatment for Arve but not for Russell.

Canonical analyses of principal coordinates were run on each of the same five data-sets to further explore the effects of location and treatment on beetle assemblage composition, as well as to explore the issue of 'false treatment' effects, i.e., whether the differences that the analyses were able to detect comparing CBS with CBS-FW were any greater than differences comparing a 'false treatment' comprising Arve CBS and Russell CBS-FW with a 'false treatment' comprising Arve CBS-FW and Russell CBS. Statistics from the CAP analyses are given in Table 3. The analyses consistently reported highly significant differences between Arve and Russell, and the program required relatively few (four or five) principal coordinate axes while still explaining 62-69% of the variation in the multivariate data. In a 'leave-one-out' allocation routine, the program experienced no misclassification error for location for any of the data-sets.

In analyses of treatment data-sets, the program required a wider range (four to ten) of principal coordinate axes to explain the variation, but in doing so explained a higher proportion (70-92%) of that variation. The statistical significance of differences between the two treatments (CBS and CBS-FW) was generally at a lower level compared to that between the two locations (Arve and Russell). The obligately saproxylic beetles data-set most clearly showed highly significant treatment differences, while the non-saproxylic beetles data-set was the only one to produce a clearly non-significant result. In 'leave-one-out' allocation routines, the program experienced misclassification errors for all treatment data-sets. The non-saproxylic beetles data-set had high misclassification rates for both CBS and

CBS-FW, consistent with there being a statistically non-significant treatment effect for this data-set. Misclassification rates were slight in the other data-sets and (apart from the facultative data-set) were confined to the CBS treatment, suggesting that beetle assemblage composition in CBS-FW was more consistent than that of CBS.

The analyses of 'false treatment' datasets required an even wider range (four to twelve) of principal coordinate axes to explain the variation, but in doing so explained the highest proportion (69-95%) of that variation. The analyses produced statistically non-significant results for the allbeetles and all-saproxylic-beetles data-sets, despite the relatively high allocation success rate. For the other saproxylic data-sets, statistically significant results suggest that the program was able to successfully classify them into the two 'false treatment' groups, but it did so with lower levels of allocation success than for the 'real treatment' datasets. The program apparently found it easier to classify the non-saproxylic dataset into 'false treatments' than into 'real treatments', since it obtained a statistically significant result with a concomitant higher allocation success rate. The additional use of these 'false treatment' data-sets allows one to conclude that the preceding analyses on 'real treatment' data-sets presented convincing differences between treatments (and between locations) for saproxylic datasets, but not for non-saproxylic data-sets.

Discussion

Before considering treatment effects, it is important to first comment on the finding that location-level differences gave a much stronger signal than treatment differences in every multivariate data-set. Stronger location-level differences than treatment differences imply that the beetle faunas of Russell and Arve differ more markedly than do the beetle faunas of CBS and CBS-FW. This highlights the desirability of much greater site replication in studies of

Table 3. Results of canonical analyses of principal coordinates (CAP) examining the effects of location and treatment on beetles from a range of data-sets derived from four study sites at two locations in Tasmania's southern forests used to examine the effects of past fuelwood harvesting on beetles. Sx = saproxylic; Fac = facultative; Obl = obligate; Trt = treatment; F-trt = 'false treatment'.

Factor	Data-set	Number of principal coordinate axes	% of variation explained by axes	Allocation success: Group 1 (%)	Allocation success: Group 2 (%)	Total allocation success (%)	Squared canonical correlation	р
Site	All	5	64	100 (Arve)	100 (Russell)	100	0.966	0.0001
	All sx	5	64	100 (Arve)	100 (Russell)	100	0.971	0.0001
	Fac sx	4	62	100 (Arve)	100 (Russell)	100	0.945	0.0001
	Obl sx	4	63	100 (Arve)	100 (Russell)	100	0.907	0.0002
	Non sx	4	69	100 (Arve)	100 (Russell)	100	0.849	0.0002
Trt	All	9	70	88 (CBS)	100 (FW)	94	0.934	0.0073
	All sx	9	86	88 (CBS)	100 (FW)	94	0.922	0.0113
	Fac sx	10	92	88 (CBS)	75 (FW)	81	0.916	0.0355
	Obl sx	6	77	88 (CBS)	100 (FW)	94	0.885	0.0007
	Non sx	5	77	50 (CBS)	63 (FW)	56	0.438	0.2623
F-trt	All	12	95	88	75	81	0.957	0.0923
	All sx	11	93	88	88	88	0.935	0.0613
	Fac sx	6	75	50	63	56	0.730	0.0244
	Obl sx	9	91	75	88	81	0.889	0.0270
	Non sx	4	69	75	75	75	0.586	0.0363

this nature, to ensure that any treatment effects are not overwhelmed by site effects. Unfortunately the scarcity of suitable study sites is not readily overcome, since it is a consequence of there having been little historical fuelwood harvesting in this region on which to base such a study.

Confounding the interpretation limitations imposed by the low level of location replication are the between-location and within-location spatial separation, the between-location altitudinal differences, and the between-location and within-location differences in time since disturbance. Sometimes location and treatment effects were themselves confounded, as in the case of the facultatively saproxylic dataset, where treatment effects were apparent in the unconstrained ordination for Arve but not for Russell. It remains possible that the stronger apparent treatment effect at Arve compared to Russell may be attributable to the Arve sites being over a kilometre apart and therefore embedded in slightly different local species pools. More obviously, the findings suggest that there is a high degree of beetle species turnover (i.e. change in the composition of the local species pool) over physical distance (i.e. between the two locations). The altitudinal differences between the two locations is a further confounding factor that is also likely to have an influence on beetle assemblage composition. The temporal separation between the two treatments at Arve, where there is a seven year age-difference in the forest regeneration, may also account for the stronger apparent treatment effect at Arve compared to Russell. Likewise, the age differences between Russell and the two Arve sites may account for some of the locational differences.

Despite these additional signals in the data, this study has enabled some preliminary conclusions to be drawn on the additional impacts of fuelwood harvesting over and above CBS. To summarise, this study has found:

- Fewer saproxylic beetles in CBS-FW compared to CBS.
- Fewer species of both obligately and facultatively saproxylic beetles at Arve, and fewer species of obligately saproxylic beetle at Russell, in CBS-FW compared to CBS
- More species of non-saproxylic beetles in CBS-FW compared to CBS.
- Different assemblages of saproxylic beetles, but not of non-saproxylic beetles, in CBS-FW compared to CBS.
- Obligately saproxylic beetle species being represented by fewer individuals per species than is the case for facultatively saproxylic species.
- Obligately saproxylic beetle species contributing substantially more to the differences in assemblage composition between CBS-FW and CBS in spite of their low numbers.

Consistently lowered abundance of saproxylic beetles, but no consistently lowered abundance of non-saproxylic beetles, in CBS-FW compared to CBS is perhaps an indication of a potential negative effect of fuelwood harvesting. One would expect that lowered resource availability (in this case, less CWD) would lead to lowered abundance of organisms (in this case, saproxylic beetles) that utilise that resource. One would further expect that this would be reflected in lower sample sizes in traps situated in the general area, since it is assumed that these traps are catching individuals dispersing between logs in the vicinity.

A negative impact of fuelwood harvesting is further suggested by the presence of fewer saproxylic beetle species in CBS-FW compared to CBS. The trend was apparent among both obligately and facultatively saproxylic beetles at Arve, but in only obligate species at Russell, so the effect, if real, may be weak. It nevertheless fits with expectations from studies elsewhere, in which species richness of saproxylic beetles has been shown to be positively related to the amount of CWD in the vicinity (e.g. Sweden: Ranius and Jonsson (2007); Germany: Müller *et al.* (2007); NE Queensland: Grove (2002b)).

Saproxylic beetle assemblage composition in CBS-FW was found to be subtly, but significantly, different compared to CBS. The clearest separation in assemblage composition between CBS-FW and CBS is shown by the obligately saproxylic beetle species data-set (Figure 3e), and it seems that these are contributing greatly to the observed separations in other data-sets that include obligate species. Comparing the results for the 'false treatment' data-sets with the 'real treatment' data-sets supports the attribution of the differences between CBS-FW and CBS to a genuine treatment effect. For those saproxylic beetle data-sets for which the CAP program was able to find statistically significant differences (Table 3), the differences were more stark with the 'real' data-sets. While there remains the possibility that the apparent treatment differences are instead attributable to factors not explored in the study, it is notable that there is no significant separation by treatment for the non-saproxylic beetle species data-set, even in a constrained ordination. This difference between non-saproxylic and saproxylic data-sets suggests, but cannot prove, that fuelwood harvesting is a cause of the effect detected for saproxylic beetles.

The clearer separation of the obligately saproxylic beetle assemblages than of the facultatively saproxylic beetle assemblages is consistent with their respective resource requirements. In the local context (i.e. young regenerating forest derived from CBS), dead wood only exists in the form of CWD on the ground (i.e. there are no large old trees left standing in the coupes). This means that the obligately saproxylic beetles have no other resource to exploit than the remaining CWD, whereas the facultatively saproxylic species presumably do (leaf litter and fine woody debris). Nevertheless, it should not be assumed that facultatively saproxylic species can get by without CWD. In a study in Slovakia, Topp *et al.* (2006) found that the abundance and species richness of litter-dwelling beetles (a category presumably including many facultatively saproxylic species) peaked in the presence of CWD. Furthermore, in Sweden, fine woody debris is targeted as fuelwood (because there is little CWD, and most is protected from harvest). In this situation, Jonsell et al. (2007) found that even fine woody debris supports its own characteristic species of beetles, which they concluded could be threatened by fuelwood harvesting.

The trend for obligately saproxylic species to generally occur at lower abundance than facultatively saproxylic species may be another aspect of their possibly greater sensitivity to reductions in CWD brought on by fuelwood harvesting. However, this would assume equal susceptibility to being collected using the techniques employed in this study. An alternative explanation is that the sampling techniques used in this study may preferentially catch facultatively saproxylic species, because they might be expected to move around in the general vicinity of CWD more than would obligately saproxylic species and hence might encounter the traps more readily. Note, however, that a lowered availability of CWD is unlikely to account for the even lower abundance of non-saproxylic species, although the study suggests no alternative explanations.

It should also be borne in mind that each study area was only a matter of a few tens of hectares in extent. Thus it is possible that any treatment effect may have been dampened by the degree to which breeding habitat (CWD) was available (or not) in the surrounding landscape, beyond the coupe boundary but still within the dispersal range for some of the species sampled. As Jonsell (2007) notes in a Swedish study, the effects of fuelwood harvesting, if sufficiently widespread in the production forest landscape, are likely to manifest at scales much broader than the area of individual harvesting units. In Tasmania, in the absence of broadscale fuelwood harvesting at present, the corollary is also likely to be true.

Given the limited past scale of fuelwood harvesting in the region, it would not be possible to increase the statistical power of this research approach markedly by expanding it to a much wider number of locations. Instead, molecular studies looking at the population genetics of a range of saproxylic species with different habitat requirements and dispersal abilities could offer a more targeted approach to understanding issues of CWD connectivity and continuity in the production forest landscape. Such a study need not be confined to comparing CBS-FW with CBS, and could make use of a much wider range of forest ages and disturbance types, and hence need not suffer from the same lack of statistical power. The presence of at least one threatened saproxylic beetle species (Lissotes menalcas) in the study area (and in the southern forests more generally) gives an added incentive to ensuring that these issues are adequately addressed.

Conclusion

The limited scale of past fuelwood harvesting makes it difficult to draw firm conclusions about its impact on saproxylic beetles. However, trends in abundance and assemblage composition in various components of the overall sampled beetle data-set strongly suggest an impact of fuelwood harvesting on saproxylic beetles over and above that of CBS. These findings are consistent with expectations, but need to be treated with caution given the limited scope of the study. They are perhaps best viewed as supportive evidence available to be combined with findings from related research projects to give guidance as to the likely extent of negative impacts of future fuelwood harvesting and ways in which these impacts can be mitigated.

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	Number of beetle individuals					
		Arve	Arve	Russell	Russell	
	Status	CBS	CBS-FW	CBS	CBS-FW	
DYTISCIDAE						
Megaporus hamatus	Ν	2	3	3	1	
CARABIDAE						
Agonocheila curtula	0	1	0	0	0	
Amblytelus TFIC sp 02	Ν	0	2	0	2	
Anomotarus crudelis	Ν	0	0	0	1	
Anomotarus illawarrae	Ν	0	3	0	1	
Mecyclothorax ambiguus	Ν	0	0	6	30	
Notonomus politulus	Ν	0	0	1	0	
Pentagonica vittipennis	Ν	2	2	1	0	
Pseudoceneus sollicitus	Ν	0	1	0	2	
Rhabdotus reflexus	Ν	7	12	4	2	
Sarothrocrepis benefica	Ν	0	1	0	0	
Scopodes sigillatus	Ν	1	3	2	1	
Scopodes tasmanicus	Ν	0	2	1	0	
Sloaneana tasmaniae	Ν	0	1	0	0	
Trechimorphus diemenensis	F	8	31	12	15	
Trigonothops pacifica	Ν	0	0	13	1	
HYDROPHILIDAE						
Notocercyon ANIC Hansen sp 01	Ν	2	1	4	5	
Notocercyon TFIC sp 01	Ν	0	1	0	0	
PTILIIDAE						
Ptiliidae TFIC sp 01	F	0	0	0	1	
Ptiliidae TFIC sp 06	F	60	17	4	0	
Ptiliidae TFIC sp 07	F	66	0	0	0	
Ptiliidae TFIC sp 08	F	0	35	81	32	
Ptiliidae TFIC sp 09	F	8	1	0	0	
Ptiliidae TFIC sp 10	F	1	0	0	0	
LEIODIDAE						
Agyrtodes tasmanicus	F	4	0	0	0	
Catoposchema tasmaniae	F	1	4	14	13	
Choleva TFIC sp 01	F	39	9	1	0	
Colenisia TFIC sp 01	F	4	6	48	48	
Colon TFIC sp 03	Ν	242	186	118	322	
Colon TFIC sp 04	Ν	1	0	0	1	
Colon TFIC sp 05	Ν	3	0	0	0	
Colon TFIC sp 06	Ν	0	0	3	0	
Colon TFIC sp 08	Ν	3	6	4	16	
Colon TFIC sp 12	Ν	0	1	0	0	
Colon TFIC sp 13	Ν	1	3	2	2	

Appendix 1. Total numbers of beetle individuals collected by study site, presented in taxonomic order. Status: N = non-saproxylic; F = facultatively saproxylic; O = obligately saproxylic. CBS = clearfell, burn and sow without fuelwood harvesting; CBS-FW = clearfell, burn and sow accompanied by fuelwood harvesting.

Number of beetle individuals Arve Arve Russell Russell Status CBS CBS-FW CBS CBS-FW Colon TFIC sp 14 N Colon TFIC sp 16 Ν Ν Colon TFIC sp 17 Colon TFIC sp 18 Ν Colon TFIC sp 20 N Eublackburniella TFIC sp 01 F F Nargiotes gordoni F Nargomorphus confertus F Nargomorphus consimilis F Nargomorphus globulus Nargomorphus jeanneli F F Nargomorphus leanus F Nargomorphus nitidus F Nargomorphus victoriensis Neopelatops TFIC sp 01 F Sogdini 'ANIC gen B' TFIC sp 01 F Sogdini SEAGO 'gen nov A' TFIC sp 01 N Sogdini TFIC sp 03 Ν Zeadolopus TFIC sp 01 N *Zeadolopus* TFIC sp 02 F **SCYDMAENIDAE** F Scydmaenidae spp **STAPHYLINIDAE** Aleocharinae TFIC sp 05 Ν F Anabaxis CHANDLER 'Type 1' F Anotylus TFIC sp 04 Aulaxus CHANDLER 'Tasmania 1' F F Austrorhysus TFIC sp 01 F Baeocera TFIC sp 01 F Baeocera TFIC sp 02 Eupinella tarsalis F F Gerallus CHANDLER 'Tasmania 1' F Homalotrichus TFIC sp 01 F Ischnosoma TFIC sp 01 F Logasa CHANDLER 'Tasmania 1' Macroplectus CHANDLER 'Type 1' F F Metacorneolabium darlingtoni? Microsilpha ANIC Thayer sp 15' Ν Palimbolus victoriae F Paraplectus CHANDLER 'Tasmania 1' F Pselaphinae TFIC sp 10 F F Rybaxis parvidens F Rybaxis variabilis F Sagola rugicornis

		Number of beetle individuals				
		Arve	Arve	Russell	Russell	
	Status	CBS	CBS-FW	CBS	CBS-FW	
Scaphidium alpicolum	0	3	8	3	9	
Scaphisoma indutum	О	11	4	4	3	
Scaphisoma TFIC sp 01	О	8	3	2	0	
Startes CHANDLER 'Tasmania 1'	F	1	2	7	6	
Washpool CHANDLER 'Tasmania 1'	О	1	0	0	0	
LUCANIDAE						
Lissotes bornemisszai	0	0	0	4	0	
Lissotes cancroides	0	2	12	8	9	
Lissotes menalcas	0	1	0	0	0	
Lissotes subcaeruleus	0	2	0	2	1	
SCARABAEIDAE						
Heteronyx dimidiatus	Ν	0	2	0	0	
Heteronyx monticola	Ν	0	1	0	0	
Heteronyx pilosellus	F	2	1	3	6	
Heteronyx pubescens	Ν	4	7	16	21	
Heteronyx TFIC sp 03	Ν		3			
Onthophagus fuliginosus	Ν	0	24	0	0	
Onthophagus mutatus	Ν	0	3	3	5	
<i>Phyllochlaenia</i> TFIC sp 01	F	2	3	0	0	
Phyllochlaenia villosus	F	3	3	0	1	
Saprosites mendax	О	0	0	1	0	
Saprus griffithi	0	13	3	8	11	
Telura vitticollis	0	5	11	37	47	
EUCINETIDAE						
Eucinetus TFIC sp 02	Ν	0	1	0	0	
Eucinetus TFIC sp 04	Ν	0	3	2	6	
CLAMBIDAE						
Clambus bornemisszai	F	8	1	1	1	
Sphaerothorax tasmani	F	14	3	2	2	
SCIRTIDAE	_	_				
Prionocyphon TFIC sp 01	0	5	0	2	0	
Pseudomicrocara atkinsoni?	F	61	114	112	40	
Pseudomicrocara TFIC sp 01	F	7	0	0	0	
Pseudomicrocara TFIC sp 02	F	3	1	0	0	
Pseudomicrocara TFIC sp 03	F	0	1	0	0	
Pseudomicrocara TFIC sp 05	F	2	0	0	1	
Scirtidae TFIC sp 01	F	0	0	1	0	
Scirtidae IFIC sp 06	F	3	0	0	1	
Sciridae IFIC sp 13	F T	3	0	U	U	
SCIFICARE IFIC SP 15	F	1	0	U	U	
BYKKHIDAE	ът	2	0	0	1	
iviicrochaetes scoparius	IN	3	U	U	1	
	ът	1	0	0	0	
Eimidae IFIC sp 01	N	1	0	U	U	

Number of beetle individuals Arve Arve Russell Russell CBS CBS-FW CBS CBS-FW Status EUCNEMIDAE Neocharis MUONA sp 01 THROSCIDAE Aulonothroscus elongatus ELATERIDAE F Agrypninae TFIC sp 01 Conoderus australasiae N Conoderus cordieri? N n Conoderus TFIC sp 03 Ν F Crepidomenus TFIC sp 03 Crepidomenus TFIC sp 05 F Denticollinae TFIC sp 01 Denticollinae TFIC sp 19 Denticollinae TFIC sp 20 Elateridae TFIC sp 05 F Elateridae TFIC sp 25 N F Elatichrosis trisulcata F *Enischnelater specularis* F Enischnelater TFIC sp 01 Parablax sp nr ossa F *Paracardiophorus* sp nr *bicolor* Ν Pityobiinae TFIC sp 02 Ο Toorongus jugulatus LYCIDAE Metriorrhynchus erythropterus? Ο Metriorrhynchus simplicornis F Porrostoma atratus F Porrostoma moerens F Porrostoma rhipidium Porrostoma rufipennis F Xylobanus insignipennis CANTHARIDAE Chauliognathus lugubris Ν Heteromastix nigripes О Heteromastix pauxillus Heteromastix perabundans Ο Heteromastix tenuis? Heteromastix TFIC sp 05 О Ο Heteromastix victoriensis DERODONTIDAE Nothoderodontus darlingtoni DERMESTIDAE Orphinus TFIC sp 01 О Trogoderma rigua Ο

Number of beetle individuals Arve Arve Russell Russell Status CBS CBS-FW CBS CBS-FW *Trogoderma* TFIC sp 01 ANOBIIDAE Anobiidae TFIC sp 13 Hadrobregmus areolicollis F Lasioderma serricorne TROGOSSITIDAE Egolia variegata CLERIDAE Blackburniella hilaris О Eunatalis porcatus Lemidia cf villosa Lemidia cicatricosa Lemidia vulchella Lemidia simsoni Lemidia suhaenea Neoscrobiger patricius Neoscrobiger rauciceps О Parapylus bicinctus MELYRIDAE Flabellolaius? TFIC sp 01 F Helcogaster TFIC sp 01 F SPHINDIDAE F Aspidiphorus humeralis Notosphindus slateri F NITIDULIDAE Amlearcha obscurior? F Soronia superba F F Thalycrodes cylindricum F Thalycrodes pulchrum TASMOSALPINGIDAE Tasmosalpingus promiscuus Ν SILVANIDAE F Cruptamorpha optata Cryptamorpha TFIC sp 01 Ο Cryptamorpha TFIC sp 02 F Cryptamorpha victoriae? Ο LAEMOPHLOEIDAE Laemophloeidae TFIC sp 03 Ο PHALACRIDAE Litochrus alternans? F Parasemus TFIC sp 01 F Phalacridae TFIC sp 05 F HOBARTIIDAE Hobartius eucalypti F

	Number of beetle individuals					
		Arve	Arve	Russell	Russell	
	Status	CBS	CBS-FW	CBS	CBS-FW	
CAVOGNATHIDAE						
Cavognatha pullivora	F	5	0	0	0	
CRYPTOPHAGIDAE						
Anchicera lewisi	F	20	6	8	4	
Cryptophagidae TFIC sp 02	F	0	0	0	1	
Cryptophagus sp nr gibbipennis	О	4	13	17	6	
Cryptophagus tasmanicus	О	17	54	28	19	
EROTYLIDAE						
Thallis vinula	F	2	25	22	30	
BIPHYLLIDAE						
Diplocoelus angustulus	F	1	5	2	5	
CERYLONIDAE						
Philothermus tasmanicus	F	2	0	0	0	
COCCINELLIDAE						
Cleobora mellyi	Ν	27	9	6	23	
Rhyzobius alphabeticus	F	0	0	1	0	
<i>Rhyzobius</i> TFIC sp 04	F	0	2	0	0	
Rhyzobius TFIC sp 05	F	0	1	0	0	
<i>Rhyzobius</i> TFIC sp 11	F	1	0	0	0	
<i>Rhyzobius</i> TFIC sp 14	F	2	0	10	7	
<i>Rhyzobius</i> TFIC sp 15	F	9	3	0	2	
Rhyzobius TFIC sp 21	F	2	1	1	0	
Stethorus TFIC sp 01	Ν	0	1	0	0	
CORYLOPHIDAE						
Holopsis TFIC sp 01	F	4	0	1	0	
Sericoderus TFIC sp 02	F	6	0	1	0	
Sericoderus TFIC sp 04	F	1	1	0	6	
Sericoderus TFIC sp 05	F	221	557	146	198	
Sericoderus TFIC sp 06	F	0	0	20	0	
LATRIDIIDAE						
Aridius nodifer	F	452	380	170	125	
Bicava maculicollis	F	1	0	0	0	
Cartodere constricta	F	0	1	2	0	
Cortinicara REIKE sp nov 1	F	31	81	14	48	
Cortinicara TFIC sp 01	F	2	10	18	6	
Cortinicara TFIC sp 02	F	0	0	0	1	
Enicmus priopterus	F	782	508	44	52	
Enicmus REIKE sp nov 1	F	102	482	433	190	
Enicmus REIKE sp nov 2	F	0	1	0	0	
Enicmus REIKE sp nov 3	F	1	7	1	4	
Enicmus spp indet	F	2	10	0	0	
MYCETOPHAGIDAE						
Litargus intricatus	F	0	0	2	5	

	Number of beetle individuals					
		Arve	Arve	Russell	Russell	
	Status	CBS	CBS-FW	CBS	CBS-FW	
CIIDAE						
Ciidae TFIC sp 01	О	2	0	1	4	
Ciidae TFIC sp 04	О	7	5	1	1	
Ciidae TFIC sp 06	О	0	3	9	0	
MELANDRYIDAE						
Callidircaea venusta	0	2	1	4	9	
Melandryidae TFIC sp 03	0	1	7	0	0	
Orchesia alphabetica	О	1	1	0	1	
Orchesia eucalypti	О	5	1	1	0	
Orchesia minuta	О	3	2	2	2	
MORDELLIDAE						
Mordella promiscua	О	1	4	2	1	
Mordella TFIC sp 01	О	0	0	0	1	
RHIPIPHORIDAE						
<i>Rhipidioides</i> TFIC sp 01	Ν	26	0	1	0	
ZOPHERIDAE						
Ablabus bicolor	0	1	0	0	0	
Latometus differens	0	8	7	4	5	
Penthelispa fuliginosa	0	1	2	0	5	
TENEBRIONIDAE		4	2	0	0	
Adelium abbreviatum	0	1	3	0	0	
Atoichus tasmanicus	0	0	1	0	1	
Coripera deplanata	0	0	3	0	1	
PROSIOMIDAE	0	1	07	0	22	
Prostomis atkinsoni	0	1	27	8	23	
Debenie wirzude	0	0	2	2	0	
Dohrnia miranaa Dohrnia simulas	0	62	3 190	2	0	
	0	03	160	23	4	
Rinhurrum ruficellie	0	0	1	4	2	
SAL PINCIDAE	0	0	1	4	3	
Neosalningus hubridus	0	6	8	8	12	
ANTHICIDAE	0	0	0	0	12	
Trichananca victoriensis	N	0	1	1	0	
ADERIDAE	1	0	Ŧ	1	0	
Aderidae TFIC sp 05	0	1	2	0	0	
Aderidae TFIC sp 06	0	1	- 1	1	0	
Aderidae TFIC sp 07	0	0	1	1	0	
Aderidae TFIC sp 08	0	0	10	13	4	
SCRAPTIIDAE	Ũ	Ū	10	10	Ŧ	
Scraptia laticollis	0	3	0	1	0	
Scraptia TFIC sp 01	0	4	4	1	0	
Scraptiidae TFIC sp 01	Ō	0	0	1	0	
,	-	-	-	-	-	

		Number of beetle individuals					
		Arve	Arve	Russell	Russell		
	Status	CBS	CBS-FW	CBS	CBS-FW		
CERAMBYCIDAE							
Aphneope quadrimaculator	0	0	0	2	0		
Bethelium signiferum	О	1	0	0	0		
Dorcadida bilocularis	О	0	0	0	3		
Enneaphyllus aeneipennis	0	6	0	3	3		
Homaemota walkeri	0	1	0	0	0		
Mecynopus cothurnatus	0	0	1	0	3		
Phalota TFIC sp 01	0	0	0	0	1		
Uracanthus triangularis	0	0	2	0	0		
CHRYSOMELIDAE							
Aporocera viridis	Ν	0	1	0	0		
Arsipoda erichsoni	Ν	1	0	4	5		
Arsipoda variegata	Ν	1	1	4	1		
Bruchidius TFIC sp 01	Ν	0	0	1	0		
Eboo viridula	Ν	0	1	0	0		
Eurispa vittata	Ν	0	0	1	0		
<i>Geomela</i> TFIC sp 01	Ν	2	0	0	0		
Microdonacia octodentata	Ν	6	0	109	153		
Monolepta TFIC sp 01	Ν	0	13	0	0		
Paropsisterna bimaculata	Ν	2	4	12	22		
Peltoschema orphana	Ν	1	0	0	0		
ANTHRIBIDAE							
Anthribidae ZIMM genus J sp 01	О	0	0	1	0		
Commista bispina	О	1	0	0	1		
<i>Telala</i> ? TFIC sp 01	О	0	0	2	0		
<i>Xynotropis</i> TFIC sp 01	О	2	0	2	0		
<i>Xynotropis</i> TFIC sp 02	О	0	0	1	1		
BELIDAE							
Isacantha dermestiventris	Ν	0	1	1	0		
ATTELABIDAE							
Auletobius melanocephalus	F	2	0	0	0		
Auletobius suturalis?	Ν	1	0	0	3		
Auletobius TFIC sp 01	Ν	1	0	1	1		
BRENTIDAE							
Apion tasmanicum	Ν	2	0	30	23		
CURCULIONIDAE							
Acacicis abundans	О	0	0	1	2		
Ancyttalia oleariae	0	7	1	7	3		
Ancyttalia tarsalis	0	0	1	0	0		
Aterpodes kubus	Ν	2	0	0	0		
Cossoninae TFIC sp 06	О	1	0	0	0		
Cryptorhynchinae TFIC sp 03	0	4	1	4	0		
Cryptorhynchinae TFIC sp 10	0	1	0	0	0		
Cryptorhynchinae TFIC sp 23	0	0	0	0	1		

		Numb	er of beetle in	dividuals	
		Arve	Arve	Russell	Russell
	Status	CBS	CBS-FW	CBS	CBS-FW
Cryptorhynchinae TFIC sp 25	0	0	0	0	1
Cryptorhynchinae TFIC sp 35	О	0	0	1	1
Decilaus lateralis	О	6	0	2	1
Decilaus nigronotatus	О	6	0	1	0
Decilaus striatus	О	2	0	0	0
Decilaus TFIC sp 15	О	0	0	1	0
Diabathrariinae TFIC sp 01	Ν	0	0	1	0
Dinichus terreus	О	5	0	0	0
Elleschus wellingtoniensis	О	1	0	1	1
<i>Emplesis</i> TFIC sp 01	О	0	1	0	0
Exeiratus TFIC sp 01	F	0	0	1	0
Exithius capucinus	О	0	0	2	4
Exithius loculiferus	0	0	0	0	1
Hylastes ater	О	1	0	0	0
Listronotus bonariensis	Ν	0	0	1	0
Mandalotus muscivorus	F	5	2	13	35
Mandalotus TFIC sp 13	F	0	12	0	0
Microcryptorrhynchus pygmaeus	О	0	0	0	1
Orthorhinus TFIC sp 01	0	0	0	1	4
Pentarthrum TFIC sp 03	0	1	0	0	0
Platypus subgranosus	О	1	1	0	0
Poropterus alboscutellaris	0	0	0	0	1
Poropterus antiquus	0	0	0	1	0
Poropterus melancholicus	0	0	0	0	1
Prostomus murinus	Ν	0	2	0	0
Pseudometyrus antares	0	1	4	6	9
Rhamphus acaciae	Ν	1	0	5	5
Roptoperus tasmaniensis	О	4	0	0	0
Tychiinae TFIC sp 05	F	0	2	0	1
Tychiinae TFIC sp 22	F	1	0	1	0
Tyrtaeosus ustulatus	О	0	0	7	0
Xulechinus acaciae	0	0	1	0	1