

Early impacts of disturbance on lichens, mosses and liverworts in Tasmania's wet eucalypt production forests

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Summary

The impacts of silvicultural disturbance (felling and burning) on lichens, mosses and liverworts in *Eucalyptus obliqua*-dominated wet forest in Tasmania were investigated. The study was based on presence–absence data for 452 taxa from 52 sampling events, spanning unlogged forest and disturbed, regenerating forest about 1, 3 and 5 years after disturbance. Three aspects of species composition were compared: total species richness, occurrence of pre-disturbance species in the post-disturbance flora and relative richness of ecological groups in the flora. Total species richness was the least reliable measure for evaluating changes due to disturbance.

Felling and burning in different combinations were represented in a range of silvicultural treatments applied in the study area. They produced different levels of disturbance and different microhabitats, and thereby defined the character of the cryptogamic flora. The most severe impacts occurred at burnt sites, regardless of whether the forest had been felled or not, and the least impact was found in standing, unburnt forest.

The consequences of severe disturbance were a substantial change in species composition, with a reduction, in particular, of mature wet forest species in favour of species associated with disturbance or brightly lit, exposed environments. In the lichens, the loss of old tree indicators, old forest indicators, foliicolous species, rare species of conservation significance and species indicative of a succession towards cool temperate rainforest was especially severe. Mosses and liverworts also showed a very pronounced loss of mature wet forest species. In the mosses, the presence of newcomers, represented mostly by disturbance species or species typical of open drier conditions, masked the extent of these losses. In the liverworts, there were few newcomers and the composition of the post-disturbance flora was much depleted.

Keywords: ecology; disturbance; forestry; silvicultural systems; cryptogams; lichens; mosses; liverworts; *Eucalyptus obliqua*; Tasmania

Introduction

The relationship between the diversity and floristic composition of non-vascular cryptogams (lichens, mosses, liverworts) and

various aspects of forest ecology such as continuity and age are well-recognised and supported by an extensive body of literature. Early analyses by Rose and James (1974) and Rose (1976, 1992) introduced the notion of 'indicator species' of lichens and bryophytes (mosses, liverworts) for assessing the quality of British woodlands. These concepts have been extended to other regions, notably North America and northern Europe (e.g. Lesica *et al.* 1991; Gustafsson *et al.* 1992; Goward 1994; Kuusinen 1996; Rambo and Muir 1998; Hedenås and Ericson 2000; Frego 2007; Fritz *et al.* 2008; Fritz and Brunet 2010).

Recognition that cryptogams can be used to help understand and quantify compositional and structural differences in forests has seen them applied in numerous studies of natural and managed forests. Comparisons of old growth forests with younger stands, impacts of disturbance, habitat requirements and substrate preferences, forest fragmentation, edge effects and many other aspects of forest ecology have been investigated. Cryptogams have also been included in evaluations of the impacts of forestry activities on forest ecosystems and comparisons of the effects of different silvicultural techniques (e.g. Peck and McCune 1997; Sillett and Goslin 1999; Jalonen and Vanha-Majamaa 2001; Miège *et al.* 2001; Thomas *et al.* 2001; Newmaster and Bell 2002; Nelson and Halpern 2005; Löhmus *et al.* 2006; Aubry *et al.* 2009; Perhans *et al.* 2009; Boudreault *et al.* 2013; Halpern *et al.* 2014).

In Australia, the inclusion of cryptogams in forest ecology studies is in its infancy, and much of the basic taxonomic and floristic information that underpins Northern Hemisphere studies is still being gathered. Research has concentrated on cool temperate rainforest (e.g. Ashton and McRae 1970; Kantvilas *et al.* 1985; Kantvilas 1988, 1990; Kantvilas and Minchin 1989; Kantvilas and Jarman 1993; Jarman and Kantvilas 1995a, 1995b; Milne and Louwhoff 1999; Morley and Gibson 2004, 2010; Tng *et al.* 2009) and eucalypt-dominated forests (a major source of commercial timber) (e.g. Cremer and Mount 1965; Duncan and Dalton 1982; Brasell and Mattay 1984; Ashton 1986; Pharo and Beattie 1997, 2002; Pharo and Blanks 2000; Pharo *et al.* 2004, 2009, 2013; Jarman and Kantvilas 2001a, 2001b, 2010; Kantvilas and Jarman 2004, 2006, 2012; Turner and Pharo 2005; Turner *et al.* 2006, 2011; Turner and

Kirkpatrick 2009; Hodge *et al.* 2009; Browning *et al.* 2010; Cranfield *et al.* 2011; Baker *et al.* 2014).

In Tasmania, the impetus for much of the recent work has been the establishment of a long-term ecological research site at Warra in southern Tasmania (Brown *et al.* 2001). In 1997, Forestry Tasmania commenced a trial of silvicultural systems there (Hickey *et al.* 2001, 2006; Neyland 2010; Neyland *et al.* 2012), which incorporated investigations of silviculture, soil fertility, economic considerations, worker safety, social acceptability and biodiversity. The last included a long-term study of the impacts of different silvicultural treatments on lichens, mosses and liverworts.

Assessing the impacts of disturbance associated with different silvicultural treatments at Warra is a long-term process, especially given the life-span of the dominant trees (potentially 300+ years), the age required for the forest to be considered mature (110 years, Forestry Tasmania 2009) and the proposed logging rotation (90 years, Whiteley 1999). However, data on the early impacts of disturbance, especially when compared with pre-disturbance information from the same location, offer important insights into how the flora will develop. They provide the critical basis for developing a longitudinal study (cf. Lindenmayer *et al.* 2011) into the future. In this context, the present study investigates and compares the responses of lichens, mosses and liverworts in the first five to six years

after major habitat change due to harvesting and regenerating activities in the wet eucalypt forest at Warra.

Methods

Study area

The study area (Fig. 1) for the silvicultural systems trial (SST) lies within the Warra Long-Term Ecological Research Site located about 60 km west-south-west of Hobart in southern Tasmania (Brown *et al.* 2001). The trial site occupies an area of about 200 ha on south-east facing slopes at an elevation of 50–350 m a.s.l. (Neyland *et al.* 2012), the climate is temperate maritime (Packham 1995) with a mean annual rainfall of 1450 mm (Neyland *et al.* 2012), and soils are derived mostly from Jurassic dolerite (Laffan 2001). More detailed information on the SST is available in other publications, including Brown *et al.* (2001), Hickey *et al.* (2006), Neyland *et al.* (2009a, 2009b, 2012) and Neyland (2010).

Undisturbed forest

Vascular flora

Undisturbed vegetation mostly comprised wet forest dominated by *Eucalyptus obliqua*. The eucalypts were about 50 m tall and

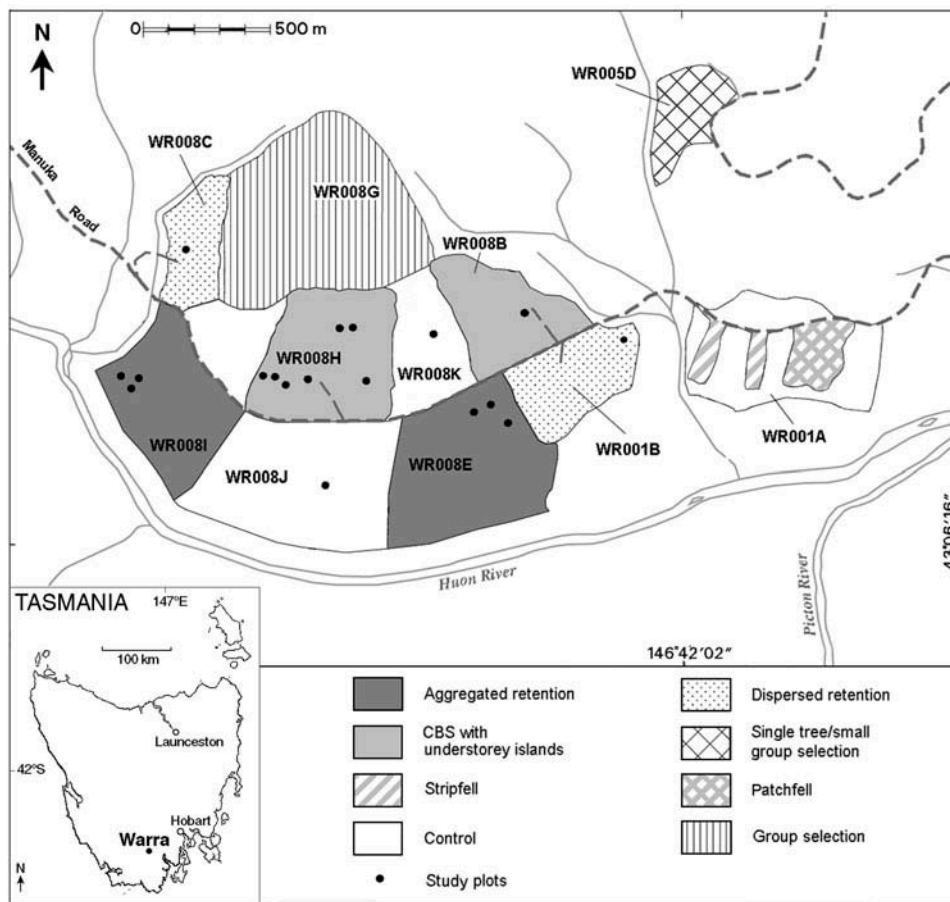


Figure 1. Location and layout of the Warra SST study area in southern Tasmania, with cryptogam plots shown within the coupes (harvesting units). (Figure modified from Jarman and Kantvilas 2010)

of mixed age, with the oldest believed to have originated from about 1500 to 1876 (Alcorn *et al.* 2001). The most widespread understorey type comprised low wet sclerophyll forest dominated by combinations of *Leptospermum*, *Melaleuca*, *Nematolepis*, *Acacia* and *Banksia* over *Gahnia* and/or *Bauera* (G-type forest, after Neyland 2001). Rainforest understoreys were also represented but were much more restricted in their distribution. More detailed information on the vascular flora is given by Neyland (2001), Jarman and Kantvilas (2001a), Kantvilas and Jarman (2004) and Neyland and Jarman (2011).

Non-vascular flora

The composition and habitat ecology of the non-vascular flora at Warra were described in detail by Jarman and Kantvilas (2001a, 2001b, 2010) and Kantvilas and Jarman (2012), where 209 lichens, 57 mosses and 106 liverworts were recorded in undisturbed forest (Kantvilas and Jarman 2012). The lichen flora was predominantly epiphytic and dominated by crustose species, with the richest families being Arthoniaceae, Pilocarpaceae (especially *Micarea*), Thelotremataceae and Cladoniaceae. The richest bryophyte families were Dicranaceae, Aneuraceae, Geocalyceae and Lepidoziaceae. The main cryptogam habitats in the undisturbed forest were the bark and wood of mature eucalypt trees (including moist faces, dry faces and buttresses), the bark of mature understorey trees and shrubs, and shaded logs, soil and rocks. A small epiphyllous flora occurred on some understorey trees and ferns.

A key feature of the cryptogamic flora in the undisturbed forest is that it appeared to be relatively young in a successional context, even though the dominant trees (eucalypts) in the forest were quite old (e.g. some over 300 years: Alcorn *et al.* 2001). In the lichen flora, for example, there was a paucity of species generally acknowledged as 'old tree indicators' (e.g. pin or calicioid lichens: Tibell 1992; Goward 1997; Selva 1998) and a near absence of species generally regarded as 'old forest indicators' (e.g. cyanolichens: Goward 1994; Kuusinen and Siitonen 1998; Goward and Arsenault 2000; Richardson and Cameron 2004). These species do occur elsewhere in Tasmania's wet forest (G. Kantvilas and J. Jarman, unpublished data) but at Warra were rare or not present in the SST plots.

The disparity between the age of the eucalypts and the cryptogam flora is attributed to fire history. Many eucalypt species can survive multiple fires, and *E. obliqua*, with its thick bark, is especially well adapted to survive such events. In the recent past, wildfires in the area have been reported for 1934, 1914 and 1898 (Alcorn *et al.* 2001). In contrast to the eucalypts, lichens and bryophytes are poorly adapted to survive fire and are consumed by flames or killed by heat, smoke and associated physiological stresses (Mistry 1998; pers. obs.). In the study area, most of those present are likely to post-date the most recent fire in the forest in 1934.

Four ecological groups are recognised within the Tasmanian cryptogam flora (Kantvilas and Jarman 2012) and all were recorded in the study area: Group 1 (mature wet forest species—old forest species, old tree species, foliicolous species); Group 2 (species of open eucalypt forests); Group 3

(ecologically widespread and common species) and Group 4 (species of disturbed habitats—transient colonisers and persistent early colonisers). A number of species were insufficiently known to be allocated to any of these groups and remain unclassified. In terms of conservation status, most of the species recorded at Warra are generally widespread and common in Tasmania's forests, either because they are generalists with a wide ecological tolerance, or specialists within a widespread habitat. However, a few species (Kantvilas and Jarman 2012) are regarded as rare in a Tasmania-wide context and are of conservation significance.

Silvicultural treatments

Silvicultural treatments employed in the SST (see Fig. 1) are outlined in Hickey *et al.* (1999, 2001, 2006), Hickey and Neyland (2000), Neyland *et al.* (2009a, 2009b, 2012), Neyland (2010) and Neyland and Jarman (2011). Aerial and ground-based views of the trial site and individual treatments are shown in Neyland *et al.* (2009b). Due to limited resources, not all treatments were utilised in this cryptogam study. Those included were:

- Clearfell, hot burn and sow (CBS) with understorey islands (CBS+UI). Four small, 40 m × 20 m islands undisturbed by machinery and amounting to about 5% by area of the coupe were retained in a coupe that was otherwise clearfelled, burnt and sown with eucalypt seed. The seed was sourced locally and aerially sown. Cryptogam plots were sampled in the islands and outside: those on the outside were treated as CBS plots.
- Dispersed retention (DRN). About 10–15% by basal area of standing eucalypts were retained within a felled area treated with a low-intensity burn and natural seedfall.
- Aggregated retention (ARN). About 30% of the forest was retained as unfelled patches of 0.5–1.0 ha within a felled area treated with a low-intensity burn and natural seedfall.
- Controls. Two coupes (harvesting units) that were excluded from forestry operations were used as silvicultural controls.

Each treatment was replicated twice (Hickey *et al.* 2001). This was achieved in terms of location (two separate coupes) but the level of replication in terms of fire behaviour and intensity was variable and probably achieved only in the hot burn treatments. Establishment of the treatments commenced in 1997 and, due to operational and commercial constraints, continued over several years (see Hickey *et al.* 2006; Neyland *et al.* 2012). Safety considerations allowed only relatively small-diameter trees to be retained in the second DRN coupe. For the lichen and bryophyte study, replication was further complicated by the time-consuming nature of sampling, and because the project was subordinate to the broader aims of the trial and to timber-harvesting schedules.

Plots and sampling

Details and discussion of the methods used, including the design, selection and location of the plots and sampling techniques can be found in Kantvilas and Jarman (2002) and Jarman and Kantvilas (2010). Eighteen plots were established (Table 1), including 12 with pre- and post-harvest data, 1 with pre-harvest

Table 1. Details of 18 plots established in the lichen and bryophyte study

| Plot | Disturbance category | Coupe | Date of burn on coupe | Sampled pre &/or post | Coupe treatment: nature of plot disturbance |
|---------------------|----------------------|--------|-----------------------|-----------------------|---|
| Middle | FB | WR008B | 26.3.00 | Pre, post | CBS+UI: felled area, hot burn |
| B471 | FB | WR008H | 7.4.01 | Pre, post | CBS+UI: felled area, hot burn |
| B372 | FB | WR008H | 7.4.01 | Pre, post | CBS+UI: felled area, hot burn |
| B518 | FB | WR008H | 7.4.01 | Pre, post | CBS+UI: felled area, hot burn |
| Bmt300 ¹ | FB | WR008H | 7.4.01 | Post | CBS+UI: felled area, hot burn |
| IaggH | FB | WR008I | 26.4.03, 21.4.04 | Post | ARN: hot burn in corridor |
| EaggH | FB | WR001E | 20.4.04 | Post | ARN: hot burn in corridor |
| Top | SB | WR008C | 9.4.00 | Pre, post | DRN: hot burn amongst standing trees |
| B106 | SB | WR008H | 7.4.01 | Pre, post | CBS+UI: island, standing burnt |
| Bn418 | SB | WR008H | 7.4.01 | Pre, post | CBS+UI: island, standing burnt |
| UI13 ¹ | SB | WR008H | 7.4.01 | Pre, post | CBS+UI: island, standing burnt |
| Small | FU | WR001B | 28.4.98 | Pre, post | DRN: cool burn and unburnt slash |
| IaggC | FU | WR008I | 26.4.03, 21.4.04 | Post | ARN: cool burn, unburnt slash in corridor |
| EaggC | FU | WR001E | 20.4.04 | Post | ARN: cool burn, unburnt slash in corridor |
| Iagg | SU | WR008I | 26.4.03, 21.4.04 | Pre, post | ARN: retained patch of standing forest |
| Eagg | SU | WR001E | 20.4.04 | Pre, post | ARN: retained patch of standing forest |
| ConJ | SU | WR008J | – | Pre, 'post' | Control: untreated standing forest |
| K688 | SU | WR008K | – | Pre | Control: untreated standing forest |

ARN, aggregated retention; CBS+UI, clearfell, burn and sow with understorey islands; DRN, dispersed retention; FB, felled, burnt; FU, felled, unburnt; SB, standing, burnt; SU, standing, unburnt.

¹Plots with a rainforest understorey: all other plots had a wet sclerophyll understorey.

data only and 5 others with post-harvest data only. The plots (Fig. 1) were spread over eight coupes, which were 11–26 ha in area, apart from one control coupe of 35 ha (Hickey *et al.* 2006; Neyland *et al.* 2012). The plots were sampled across 13 years, commencing in 1997, and comprised 52 sampling events. Sixteen plots were in wet sclerophyll forest and two in wet eucalypt forest over a rainforest understorey. Plots were 500 m², and rectangular (mostly 50 m × 10 m) or T-shaped. In most cases, location of the plots was dictated by the aims of the broader SST study, including commercial and silvicultural goals, and was not necessarily optimal for lichens and bryophytes.

A full species inventory was compiled by searching all accessible habitats (up to 2 m high on standing trunks) exhaustively (c. 6 h/plot). Special attention was given to those microhabitats where, on the basis of past experience, we could expect cryptogams to occur. Additional records from ground transects (to be analysed elsewhere) occasionally supplemented the inventories. Only presence–absence data were collected due to resource constraints, with the minutest amount of a species being scored as a 'hit'.

After harvesting, plots were resampled at approximately 1, 3 and 5 years, but with some variability due to time constraints and weather conditions. One silvicultural control was resampled at year 12; the second control had sustained damage from other forest activities and was not resampled. The absence of data from one control was not considered critical in this particular study where the emphasis was on a comparison of the three plant groups under the same conditions.

Species identification

Samples of most species were collected for checking in the laboratory. Specimens were identified according to standard procedures of microscopy, thin layer chromatography (lichens

only) and comparison with reliably identified reference specimens and published descriptions. Assistance with identifications was provided for a number of species, as acknowledged in Kantvilas and Jarman (2012). Voucher material is held at the Tasmanian Herbarium or Forestry Tasmania.

Several practical problems were encountered with species identifications in what was previously a very poorly studied flora. Taxonomic uncertainties in the literature, 'ecological scraps' in the field where tiny fragments did not yield sufficient material for identification, and difficulties with particular developmental stages hindered identification. However, our knowledge of the flora increased progressively over the 13 years of the study and hence some reconciliation was required between early and late identifications for certain taxa. These problems were treated on a case-by-case basis, resulting in a few taxa being amalgamated and others being excluded from analyses. More detailed discussion of problems associated with species identifications is given in Jarman and Kantvilas (2010).

Analyses

The study was initially intended to explore the impacts of silvicultural treatments. However, following treatment, the coupes were found to be heterogeneous, particularly at the scale affecting potential cryptogam habitats. The low number of plots that could be sampled with available resources was considered inadequate to properly represent the whole treatment. To circumvent this, the data were restratified to examine the two major disturbance factors, felling and burning, and the plots were coded accordingly: felled, burnt (FB); standing, burnt (SB); felled, unburnt (FU) and standing, unburnt (SU). The codes reflect the actual disturbance regime imposed on the plots irrespective of which formal silvicultural treatment (Table 1) had been applied to the coupe.

From a combined total of 452 cryptogam taxa recorded before or after treatment (for annotated inventory see Kantvilas and Jarman 2012), 416 were used in the analyses. These comprised 236 lichens, 74 mosses and 106 liverworts. Separate analyses were undertaken for each of the three cryptogam groups.

Trends in community composition

Community data matrices were compiled for species occurrence in each of the 52 sampling events that corresponded to combinations of plot and sampling occasion. Patterns of change in community composition were examined using ordination by non-metric multidimensional scaling or NMDS (Kruskal 1964), a method shown to be robust for community ordination and more effective than alternative techniques (Minchin 1987). Differences in community composition were expressed using the Bray–Curtis dissimilarity index (Bray and Curtis 1957), a widely used measure appropriate for community analyses (Faith *et al.* 1987). NMDS was run from 100 different random starts and the solution with the lowest stress was chosen for the ordinations. Since the appropriate number of dimensions required to effectively represent each data set was not known in advance, the entire analysis was run in one to six dimensions. Scree plots, in which minimum stress is graphed against number of dimensions, were then examined to determine the required dimensionality (McCune and Grace 2002).

To examine the trajectories of community change in each sampling plot, ordination diagrams were prepared in which the points corresponding to a given plot at different sampling times were joined by lines, starting at the pre-disturbance point and terminating at the point representing the final sampling date. Five plots had no pre-harvest data. Therefore, as the starting point, a surrogate pre-harvest plot was selected from the same vegetation type as the post-harvest plot before treatment (*UI13* for Bmt300; *Iagg* for IaggH and IaggC; and *Eagg* for EaggH and EaggC). In each case, the surrogate plot was no further than 130 m distant from post-harvest plot. The vegetation type of the surrogate plot, including its floristic and structural character, was determined from vascular plant surveys (Forestry Tasmania, unpublished data).

Analysis of Similarities or ANOSIM (Clarke 1993), a non-parametric multivariate test, was used on the pre-harvest cryptogam data to test for differences in community composition among groups of plots defined by the four disturbance categories. It was also used on the same groups of plots to test whether there were differences before disturbance and after disturbance at the final sampling occasion.

NMDS ordinations, ANOSIM tests and plotting of ordination diagrams were performed using DECODA v3 (Minchin 1998).

Changes in species richness

Three aspects of cryptogam floristic composition were investigated: total species richness; the proportion of species shared before and after disturbance and the proportion of species from each ecological group in the flora. In the second of these analyses, species were coded as: (a) those recorded only in

mature, undisturbed forest, (b) those recorded in both mature, undisturbed forest and in plots after treatment and (c) those recorded only after treatment (newcomers). In the third analysis, species were coded according to their ecological group (Kantvilas and Jarman 2012):

- (a) Group 1—mature wet forest species.
- (b) Group 2—species of open eucalypt forest.
- (c) Group 3—widespread species.
- (d) Group 4—species characteristic of disturbed sites.

Pre-harvest plots (12 wet sclerophyll, 1 rainforest) were compared with the post-harvest plots (15 wet sclerophyll, 2 rainforest) at the final sampling date, which was 4–6 years for most plots. There were three exceptions: the final sampling date for one standing, unburnt plot was 12 years, and the final sampling date for one felled, burnt plot and one felled, unburnt plot was 3 years. For the comparisons, the post-harvest plots were grouped according to the four disturbance categories: FB, SB, FU and SU (see above). In each of the three analyses, differences in mean species richness in each category (pre-harvest, FB, SB, FU, SU) were tested using one-way analysis of variance (ANOVA). Where the ANOVA showed that the means were not all equal, a Tukey–Kramer multiple comparison test with an alpha level of 0.05 was used to assess which means differed. ANOVAs were run using SAS version 9.3 (SAS Institute 2010). Three plots with a rainforest understorey (one pre-harvest, one FB and one SB) were excluded from the ANOVAs.

Results

Patterns in community change: an overview

Changes in floristic composition over time for lichens, mosses and liverworts, based on all plots from all treatments, are illustrated in Figure 2. Trajectory lines indicate the direction of change. The ordinations required two dimensions only, with the minimum stress (0.0974 for lichens, 0.0882 for mosses, 0.0962 for liverworts) being achieved from all 100 random starts in each analysis.

In each cryptogam group, plots from the pre-harvest forest are grouped at the far left of the ordinations, confirming their floristic similarity. After the initial sampling, the plots are variously distributed in the ordination space depending on the nature of the disturbance. To facilitate comparisons, the degree of floristic change produced by each disturbance regime is shown separately in Figure 3 (lichens), Figure 4 (mosses) and Figure 5 (liverworts), using subsets of plots taken from Figures 2a, 2b and 2c, respectively. An envelope representing the spread of the entire data set, based on Figure 2, is superimposed over each of the ordinations and provides a context in which to assess the relative extent of the changes.

ANOSIM tests showed that in the pre-harvest vegetation, there were no significant compositional differences between the groups of plots from the four disturbance categories (lichens, $R = -0.0901$, $P = 0.7234$; mosses, $R = -0.0054$, $P = 0.4483$ and liverworts, $R = -0.0357$, $P = 0.3788$).

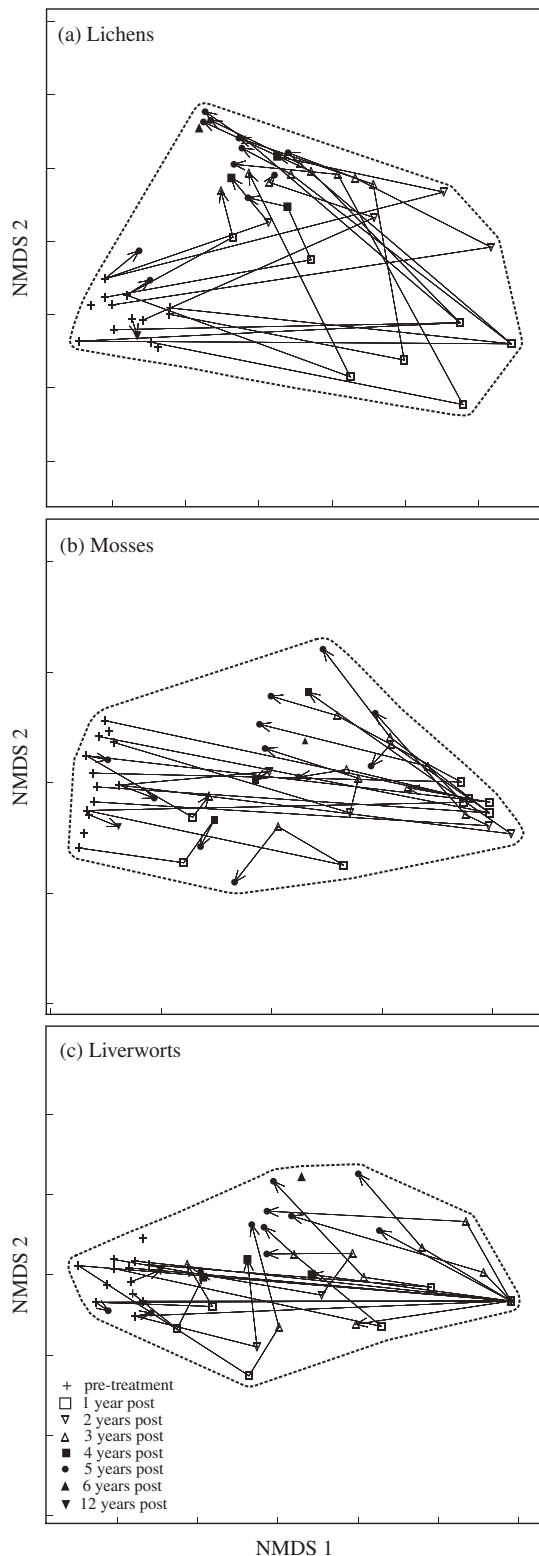


Figure 2. Two-dimensional NMDS ordination of the complete data set (52 sampling events) showing changes in floristic composition over time for (a) lichens, (b) mosses and (c) liverworts. Trajectory lines mark the direction of each plot's development over the sampling period

Lichens

In the lichens (Fig. 3), burning initially appeared to have a greater effect on species composition than felling. However, 3–4 years after disturbance, this difference was no longer

apparent, with the plots displaying a similar composition regardless of whether they had been felled and burnt (FB), standing and burnt (SB) or felled but not burnt (FU). ANOSIM tests confirmed that, at their final sampling, they each remained different from their pre-disturbance composition (Table 2, $P < 0.002$ in each case). The standing, unburnt plots (SU), which included one from the silvicultural control sampled at 12 years, were distinct from the felled and/or burnt plots, and showed little change over the sampling period.

It is noteworthy that the shift in floristic composition of the disturbed plots over the sampling period is not directly towards the original pre-disturbance composition (Fig. 3).

Mosses

For the moss flora, the main trends shown in the ordination trajectory diagrams (Figs 4a–d) and ANOSIM tests (Table 2) were essentially the same as those seen in the lichens, with the greatest changes occurring in the FB, SB and FU categories and the SU plots showing the least change. Unlike the situation for lichens, however, burning appears to be the more critical factor and FU plots showed less change when compared with burnt categories in years 1–2, and little further change after 3 years, being closer to their pre-disturbance state than either FB or SB plots. On their final sampling, ANOSIM tests indicated that FB, SB and FU each remained different from their pre-disturbance composition ($P < 0.002$ in each case, Table 2). The SU plots were also significantly different from pre-treatment composition, but barely so ($R = 0.28$, $P = 0.032$).

Compared with the lichens at their final sampling, the shift in floristic composition of the disturbed plots is more directly towards their original pre-disturbance composition (Fig. 4).

Liverworts

Trends in the liverworts were similar to those seen in mosses (Fig. 5a–d), with the most marked changes occurring in years 1–2 after burning (FB, SB). Several plots converged on a single point as their liverwort community was reduced to *Marchantia berteroana* and *Cephaloziella* species only. Again, least change was observed in the SU category. On their final sampling, ANOSIM tests confirmed that FB, SB and FU plots remained different from their pre-disturbance composition ($P < 0.005$ in each case), whereas the SU plots did not ($R = 0.16$, $P = 0.19$) (Table 2). As with mosses, the shift in floristic composition over the sampling period was more directly back towards the pre-disturbance state than shown by the lichens (Fig. 5).

Changes in species richness

The nature of the changes occurring in the flora are illustrated in Figure 6 (total species richness), Figure 7 (occurrence of pre-disturbance species in the post-disturbance flora) and Figure 8 (relative richness of the ecological groups). Data from plots with a wet sclerophyll understorey and those with a rainforest understorey are presented separately in these figures.

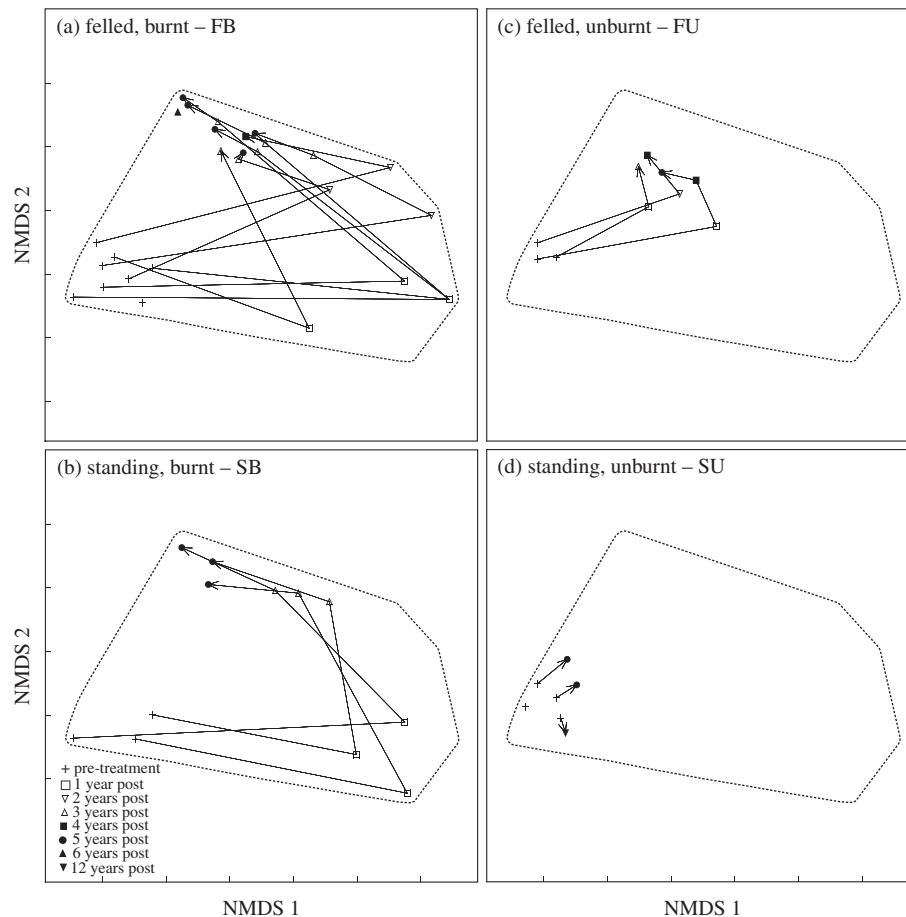


Figure 3. Changes in community composition of lichens over time, based on Figure 2a but showing separately the responses according to four disturbance categories. The dotted outline represents the spread of the entire lichen data set as shown in Figure 2a

Lichens

In wet sclerophyll forest, standing, unburnt plots (SU) were very similar to the pre-harvest forest in terms of total richness and the character of the lichen flora (Figs 6a, 7a, 8a). There was a small component of newcomers but these species were essentially due to edge effects and to disturbance from a fallen eucalypt crown.

In the other disturbance categories (FB, SB and FU), the plots had a very different composition from that in the pre-harvest forest. There was a significant reduction in pre-harvest species (Fig. 7a), which can be attributed to high losses among mature wet forest species (Group 1 species) (Fig. 8a). A high proportion of the post-harvest flora was represented by newcomers, comprising pioneers and transient colonisers (Group 4) and, to a lesser extent, open forest species (Group 2). The richness of widespread species (Group 3) did not vary before and after disturbance, although field observations indicated that the abundance of individual species was markedly reduced.

Mosses

The moss flora of unburnt plots, whether standing or felled (SU, FU), generally showed little change in overall species richness from the pre-harvest forest (Figs 6b, 7b), although individual plots (data not shown) may even have greater richness due to

the presence of newcomers. In SU plots, the standing forest provided the protection to maintain an essentially pre-harvest moss flora similar to the situation for lichens. However, edge effects enabled additional species (newcomers) to establish. In FU plots, many survivors from the pre-harvest flora occurred in protected pockets of unburnt slash. Any reduction in species numbers due to felling disturbance was compensated for by a suite of newcomers found mainly in small burnt patches in the plots.

The felled, burnt plots (FB) and standing, burnt plots (SB) had a similar moss flora after disturbance. In total richness, they were little different from the undisturbed forest (Fig. 6b) but this was due to newcomers that masked losses in the pre-harvest component of the flora. As with the lichens, there were significant losses among mature wet forest species (Group 1) (Fig. 8b). The numbers (though not the abundance) of widespread species (Group 3) remained at similar levels before and after disturbance. Newcomers mainly comprised species typical of open eucalypt forest and disturbed sites.

Liverworts

In the liverwort flora, total species richness declined from the standing, unburnt plots (SU), which have essentially the same composition as the unharvested forest, through the felled, unburnt plots (FU) and the standing, burnt plots (SB), to the

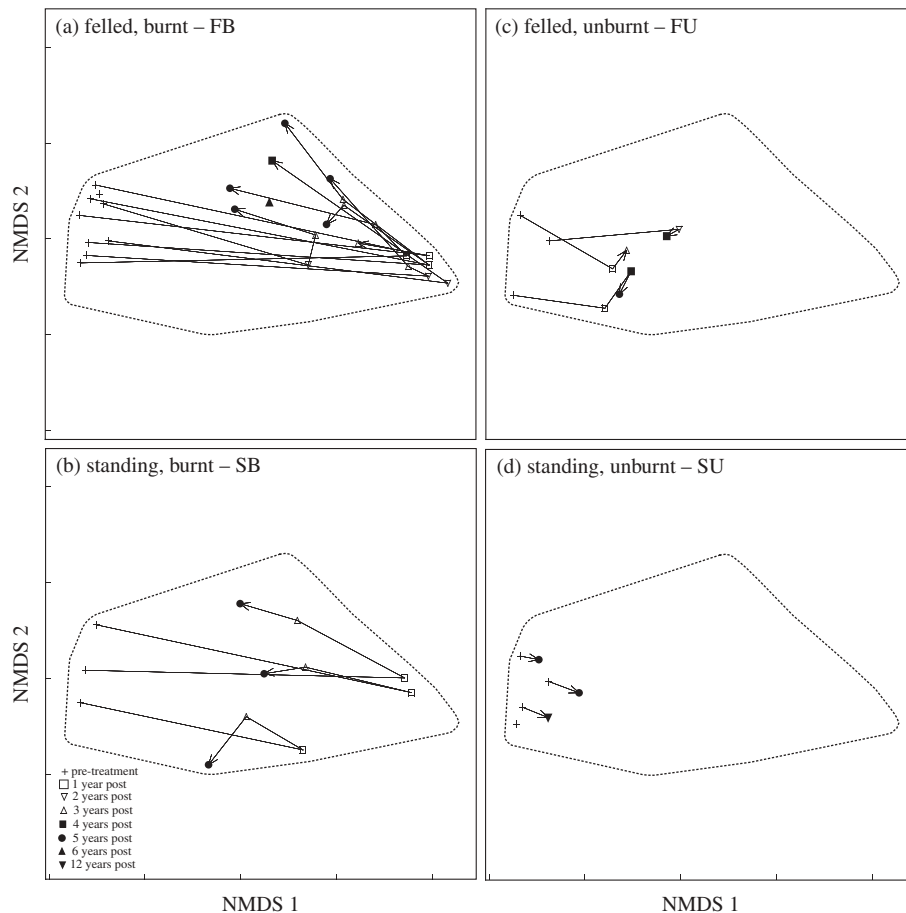


Figure 4. Changes in community composition of mosses over time, based on Figure 2b but showing separately the responses according to four disturbance categories. The dotted outline represents the spread of the entire moss data set as shown in Figure 2b

felled, burnt plots (FB), which had a very pronounced reduction in richness (Fig. 6c). As with lichens and mosses, the losses were predominantly in mature wet forest species (Group 1), which made up a very high proportion of the pre-harvest flora (Fig. 8c). Species from other ecological groups were poorly represented before disturbance and were maintained at similar levels after treatment. In contrast to the lichens and mosses, there were very few newcomers in any plots (Fig. 7c).

Discussion

Disturbance responses

Lichens, mosses and liverworts of wet forest are physically small organisms that live in an environment dominated by vascular plants. They respond to the substrates and/or habitats that vascular plants provide, either directly in the case of epiphytes or indirectly by influencing microclimatic conditions such as shade and humidity. It follows that major disturbances affecting the structure, character or composition of the vascular flora will necessarily have major impacts on the cryptogamic flora. It also means that recovery of cryptogams is inextricably linked to that of the vascular flora, but will necessarily lag behind because the cryptogams must await the development of suitable habitat conditions in the regenerating forest.

Felling and burning

Complete felling of the forest, followed by burning, produces major environmental and structural changes in wet forest ecosystems. It results in reduced habitat diversity compared with unharvested forest, including the removal of all habitats for obligate epiphytes. Surfaces available for colonisation include ash, charcoal, bleached wood, baked earth and scorched bare rock (Jarman and Kantvilas 2010), and coupled with the exposed, brightly lit environments, are largely alien and inhospitable for most forest-dwelling cryptogams (Kantvilas and Jarman 2006).

Following felling and burning, visible signs of cryptogam survivors from the undisturbed forest were extremely rare. The floristic composition of bryophytes in the first year or so after burning (Duncan and Dalton 1982; Hodge *et al.* 2009; Pharo *et al.* 2013; our own studies) suggests there are no surviving propagules of pre-fire cryptogams in the soil, although soil banks can provide a source of propagules in unburnt forests (e.g. Ross-Davis and Frego 2004). Observations suggest that lichens do not have propagules in the soil that can survive fire either. Thus, the re-establishment of a pre-disturbance cryptogam flora depends on re-entry of the species onto the site and is complicated by their dependence on the regenerating vascular flora which needs to have recovered sufficiently to provide suitable substrates and micro-environments. This process may take many years.

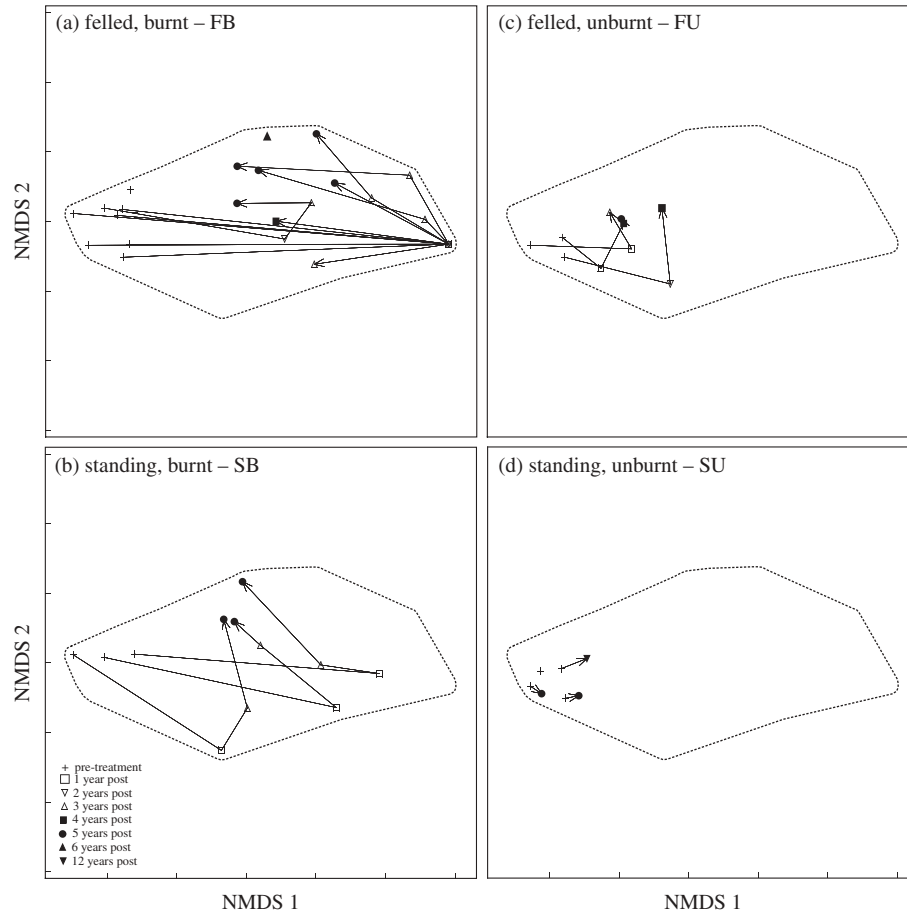


Figure 5. Changes in community composition of liverworts over time, based on Figure 2c but showing separately the responses according to four disturbance categories. The dotted outline represents the spread of the entire liverwort data set as shown in Figure 2c

Table 2. Results of ANOSIM analysis comparing community composition of groups of plots subjected to each disturbance regime at their final sampling time with their pre-disturbance composition

| Cryptogam group | Disturbance category | <i>R</i> | <i>P</i> |
|-----------------|----------------------|---------------|----------|
| Lichens | FB | 1.0000 | <0.0001 |
| | SB | 1.0000 | 0.0017 |
| | FU | 0.9991 | 0.0012 |
| | SU | 0.0721 | 0.3334 |
| Mosses | FB | 0.9967 | <0.0001 |
| | SB | 0.9886 | <0.0017 |
| | FU | 0.9050 | 0.0021 |
| | SU | 0.2802 | 0.0323 |
| Liverworts | FB | 0.9989 | <0.0001 |
| | SB | 0.9981 | 0.0021 |
| | FU | 0.7249 | 0.0041 |
| | SU | 0.1589 | 0.1834 |

The ANOSIM statistic, *R*, and its associated probability, *P*, tests the null hypothesis that community composition at the final sampling was identical to pre-disturbance composition. Significant *R* values ($P < 0.05$) are given in bold.

FB, felled, burnt; SB, standing, burnt; FU, felled, unburnt; SU, standing, unburnt.

Five years after felling and burning, lichens were less diverse and their species assemblages very different from the pre-disturbance condition (more than half were newcomers). Species

confined to old trees are particularly vulnerable. For example, there were no pin lichens (calicioid lichens) in the regenerating vegetation, which depend on very old, large trees or, at the least, on very old, large stumps and stags within a mature forest (Kantvilas and Jarman 2004).

Old forest species and foliicolous species were similarly affected. These depend on long-term forest stability, and specific light and moisture regimes. Cyanolichens typical of mature wet forests were almost eliminated. Few were present before logging, a fact attributed to past and frequent fires and resultant canopy disturbance, but they were virtually absent after logging and burning. Species of special conservation significance (e.g. *Bactrospora micareoides*, *Trichothelium meridionale* and *Cheilolejeunea comitans*; Kantvilas and Jarman 2012) were also virtually eliminated.

For mosses, there was little change in species richness following felling and burning but a substantial change in species composition, with the dominants and about one-third of the species being newcomers. In contrast, the liverwort flora was much depleted compared with its pre-burn richness.

Among the less common cryptogams in the wet sclerophyll pre-logging flora were several that are characteristic of rainforest. On a state-wide basis, these species are not considered rare since rainforest is widely distributed in the wetter parts of Tasmania. However, in the study plots, they were uncommon

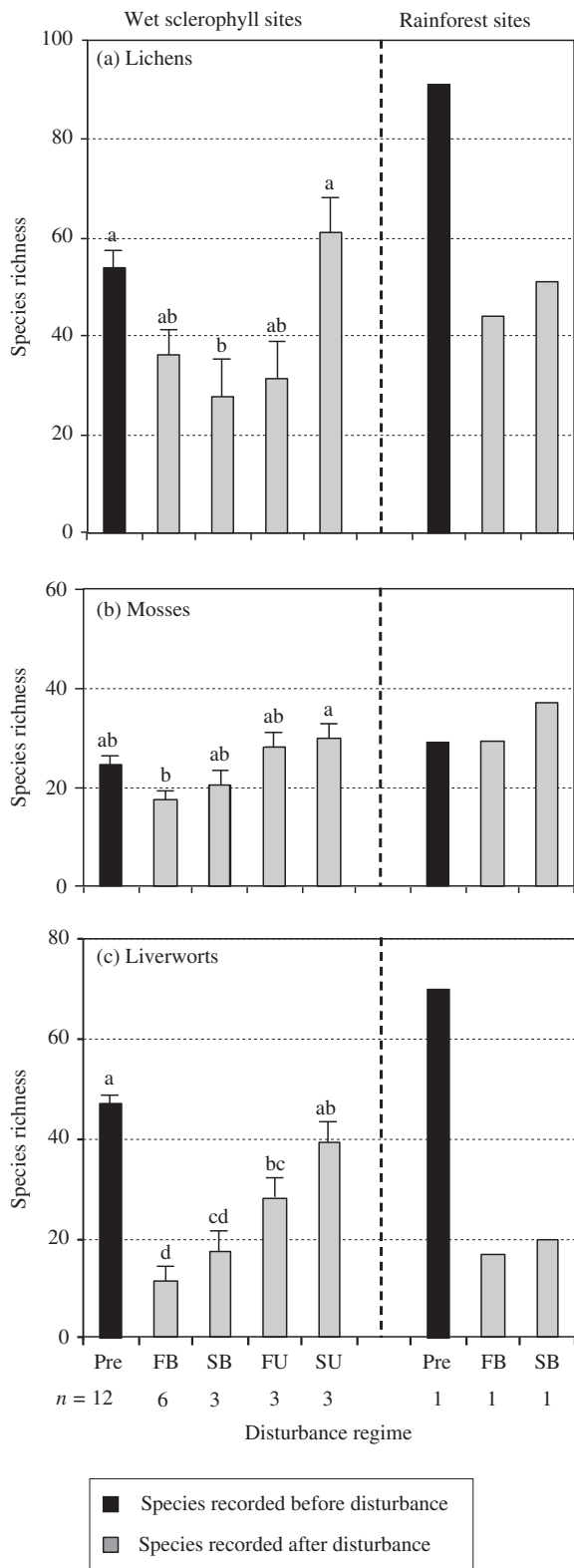


Figure 6. Total species richness for (a) lichens, (b) mosses and (c) liverworts before (Pre) and after disturbance (FB, felled burnt; SB, standing burnt; FU, felled unburnt; SU, standing unburnt). For wet sclerophyll sites, richness is represented by the mean, error bars are standard errors, and means that share the same letter within the same subset (pre-logging, lower case, or newcomers, upper case) are not significantly different ($P > 0.05$) based on Tukey–Kramer post-hoc tests

and presumably marked the beginning of a cryptogam succession from wet sclerophyll forest to rainforest, analogous to that described for vascular plants by Gilbert (1958) and Jackson

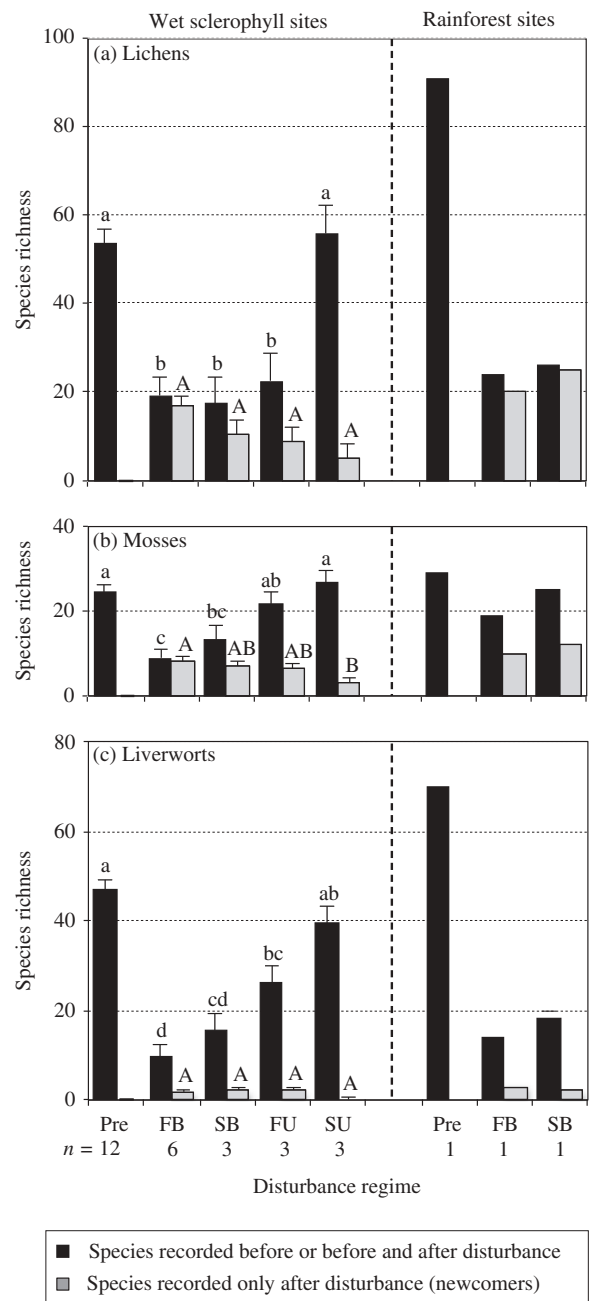


Figure 7. Species richness for (a) lichens, (b) mosses and (c) liverworts before (Pre) and after disturbance (FB, felled burnt; SB, standing burnt; FU, felled unburnt; SU, standing unburnt), with post-disturbance species partitioned into two groups indicating how many were also recorded before disturbance (pre-logging species) and how many were recorded only after disturbance (newcomers). For wet sclerophyll sites, richness is represented by the mean, error bars are standard errors, and means that share the same letter within the same subset (pre-logging, lower case, or newcomers, upper case) are not significantly different ($P > 0.05$) based on Tukey–Kramer post-hoc tests

(1968). Very few of these cryptogam species were recorded in post-fire plots, suggesting that the process of succession towards rainforest has been disrupted. The longer term implications in the context of 90-year rotations are unknown.

In the plot with a rainforest understorey, the effect of logging and burning on the cryptogams was even more severe than in wet sclerophyll understoreys. The pre-logging flora was the

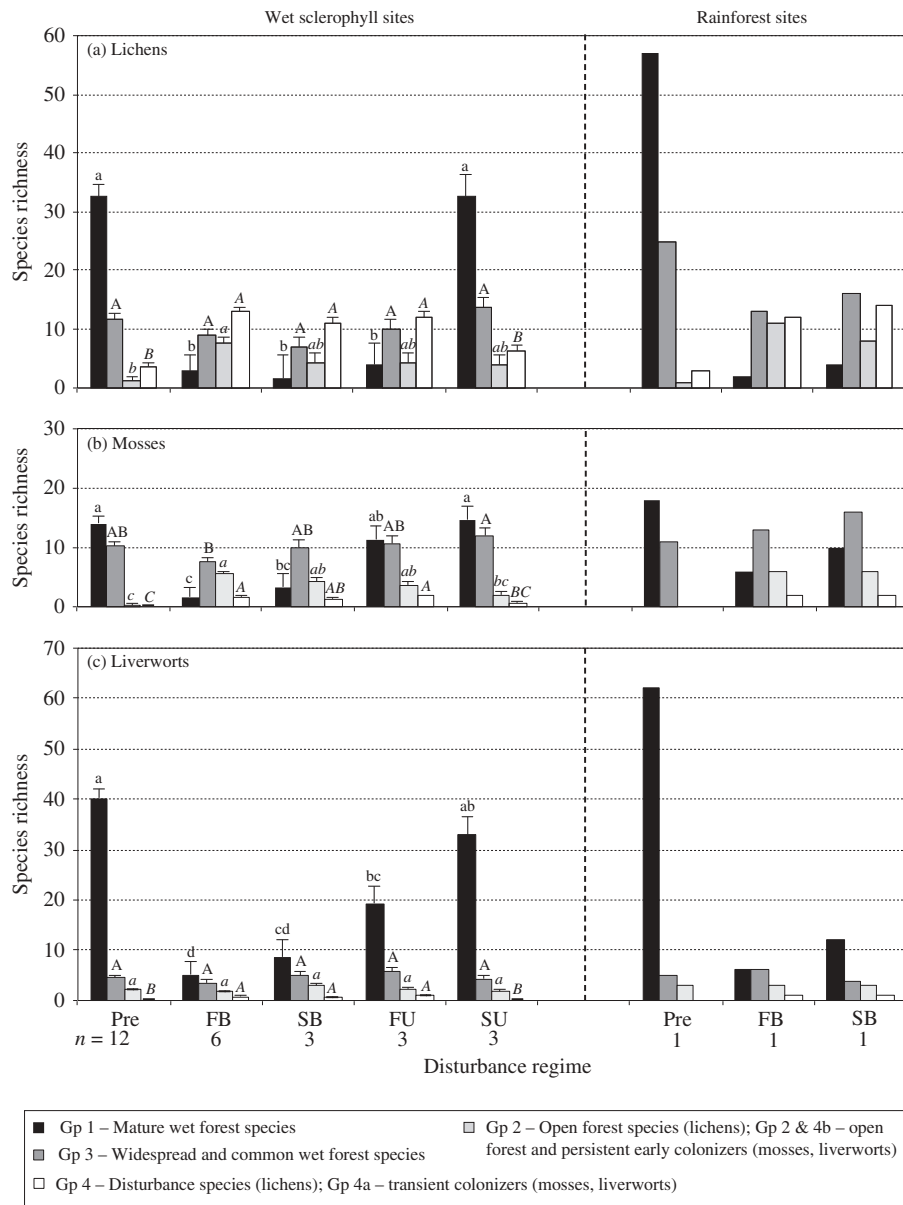


Figure 8. Species richness for (a) lichens, (b) mosses and (c) liverworts, showing relative richness of four ecological groups before (Pre) and after disturbance (FB, felled burnt; SB, standing burnt; FU, felled unburnt; SU, standing unburnt). For wet sclerophyll sites, richness is represented by the mean, error bars are standard errors, and means that share the same letter within the same subset (ecological group) are not significantly different ($P > 0.05$) based on Tukey–Kramer post-hoc tests (lower case roman—Group 1; upper case roman—Group 2; lower case italics—Group 3; upper case italics—Group 4)

most species-rich of all the plots for lichens and liverworts and the second richest for mosses, but after burning, the cryptogam flora of the plot was very similar to that of a burnt wet sclerophyll plot.

Felling and burning were part of all silvicultural treatments included in the present study. In CBS, the entire coupe was felled and burnt. In DRN, the only excluded parts were scattered standing eucalypts, some of which were heavily scorched, and patches of slash that failed to ignite. In CBS +UI, most of the coupe was felled and burnt. The islands themselves, constituting about 5% of the coupe area, were excluded from felling but some were burnt. In ARN, felling and burning occurred in the corridors, which occupied about 70% of the coupe.

Burning without felling

The response of lichens, mosses and liverworts in standing, burnt plots was rather similar to that seen in felled, burnt plots. Although standing stems of different sizes were present (dead and alive), their surfaces became charred and blackened. In many cases, the scorched bark had fallen off or will eventually do so. Most cryptogam species were completely eliminated by the fire and must enter the site from outside the plot in order to re-establish. Any survivors were at best represented by small rare fragments restricted to niches protected from the extreme heat of the fire. As in felled and burnt plots, the cryptogam flora had a greatly reduced number and abundance of mature wet forest species, and a proliferation of open forest and/or disturbance species.

In later years, standing, burnt areas would be expected to experience better cryptogam recovery than felled, burnt areas because of their greater habitat diversity. The standing structures provide future cryptogam habitats, including living and dead understorey trees as well as living and dead old growth eucalypts. Trees toppling over will result in logs, exposed unburnt soil on the root plates, and depressions and associated microhabitats at ground level. The greater structural diversity is also likely to provide better buffering of the microclimate compared to felled and burnt areas, facilitating future recolonisation by cryptogams.

Standing, burnt forest occurred in some understorey islands in the CBS+UI treatment and in some aggregates of the ARN coupes where the corridor fires had encroached into the aggregate.

Felling without burning

Plots in this category were heterogeneous in the pattern of disturbance, and while they comprised mostly unburnt slash or cleared ground, they also included small, burnt patches. No standing vegetation remained and no habitats for epiphytes were available above a few centimetres around the stumps of felled trees and shrubs.

Many mosses and liverworts can survive in unburnt forest debris, especially those species typically found in habitats low in the forest, because the debris can provide considerable protection. Even the more ecologically sensitive leafy liverworts can survive where the fallen slash has provided sheltered niches that retain a shady and relatively stable, humid environment. However, the nature of felling operations affects survival. Many cryptogams are smothered and lost if the debris is compacted. Clearing the debris (e.g. slash reduction, see Forestry Tasmania 2009), laying cording for vehicle tracks or bark for soil protection from machinery, may also result in a substantial reduction in the number of survivors.

Unlike bryophytes, lichen survival was poor in the unburnt slash. In the pre-harvest forest, lichens were predominantly epiphytic (Jarman and Kantvilas 2001a). Felling their host changes their location (position) in the forest substantially and leaves them dispossessed of a substrate when the bark peels off the fallen dead host. Even if the felled host retains its bark, the underside of fallen stems is likely to be too shaded for lichens to survive and the upper side too dry and exposed. Only a very small proportion of the mature forest lichen species are ground- or low-level forest dwellers and it is among this suite of species that most survivors were found in the unburnt slash. However, if the debris is compacted, they too may be lost due to smothering (Miège *et al.* 2001). The effect on obligately epiphytic bryophytes was similar to that on epiphytic lichens, but there were fewer of them in the flora compared to ground species, which reduced their proportional contribution to the impact on bryophytes as a whole.

Felling without burning occurred in the corridors of the ARN treatment and in one DRN coupe but was not an intended outcome. A slow burn had been planned so the felled understorey was left scattered and uncompressed on the ground,

producing a light layer of slash to facilitate the spread of fire without burning too fiercely. In the coupes studied, this resulted in a patchy fire, with areas of unburnt debris remaining in the corridors.

Neither felling nor burning

Only relatively benign levels of disturbance occurred in patches of unburnt forest standing within the logged coupes. A broad range of mature forest habitats remained essentially intact and, consequently, the floristic composition of lichens, mosses and liverworts was overwhelmingly pre-harvest in character. A small number of species was missing from the study plots 5 years later, but several of these were found in the forest surrounding the plot. Species affected most adversely were epiphytes or colonisers of dead standing wood that are dependent on a closed, undisturbed forest canopy (e.g. mature wet forest species such as calicioid lichens and species of *Micarea*). Some newcomers in the lichens and mosses were recorded after 5 years, usually near edges, or in combination with related damage from windthrow or small incursions by fire. These introductions were mostly represented by low numbers of individuals from drier, more open environments. Provided that damage in the standing forest is minimal, these species are likely to be eliminated as the surrounding vegetation develops into young forest and ameliorates the changed conditions at the edge of the patches. There was no colonisation by liverwort newcomers except where fire had entered the site.

Standing, unburnt forest occurred in aggregates that occupied about 30% of the coupe area within the ARN treatment. Smaller patches were also represented by understorey islands that had escaped fire in the CBS+UI treatment.

Comparison of lichens, mosses and liverworts

Within the Warra cryptogam flora, the most sensitive groups appear to be the lichens and the liverworts. Compared with mosses, their pre-disturbance flora included markedly more species typical of mature wet forest (Group 1 species) than any other ecological group, and there was a very pronounced reduction in the number of these species after severe disturbance (felling and burning). Such species are also very slow to re-establish. In the lichens, there was an influx of newcomers from other ecological groups, which tended to mask the high losses among the mature wet forest species. In the liverworts, there was a proliferation of a few disturbance/open forest species that were present in very low numbers in the pre-harvest forest and one short-lived dominant newcomer. With few newcomers and high losses among mature wet forest species, the composition of the liverwort flora became much depleted after disturbance.

The pre-harvest moss flora was less species rich than either the lichen or liverwort flora, and richness of mature wet forest species (Group 1) and widespread species (Group 3) was almost equal. Group 3 species are a more ecologically tolerant group and, after severe disturbance, they re-established in the regenerating forest faster than mature wet forest species. As a result, there appeared to be better proportional recovery of pre-harvest

mosses than liverworts. A comparative study of the longer term effects of wildfire versus disturbance from clearfelling and burning on bryophytes in Tasmania's wet forest (Turner and Kirkpatrick 2009) likewise suggested that mosses are not as sensitive as liverworts to silvicultural disturbance.

Where the disturbances were less extreme (felling without burning, standing aggregates in clearfells), the lichen flora was more severely affected than either the moss or liverwort flora. This is attributed, in part, to the predominance of epiphytes in the lichen flora, which occupy a location in the forest that, after felling, is completely altered or, in standing forest, is very prone to edge effects.

Vascular versus non-vascular plants

Five to 10 years after silvicultural treatment in the wet sclerophyll vegetation at Warra, the vascular flora in even the most severely disturbed sites had returned to a young wet sclerophyll forest dominated by eucalypts, with most of the pre-disturbance understorey species being present as seedlings or suckers, often in abundance. Some short-lived vascular fireweeds or disturbance species typified the regeneration in the immediate post-disturbance stage but declined as the pre-harvest wet sclerophyll community developed further (Neyland and Jarman 2011; see also studies such as Cunningham and Cremer 1965). Thus, early indications are that the pre-harvest vascular composition of wet sclerophyll forest is likely to be restored within the rotation times (90 years) proposed for the coupes. The high representation of pre-disturbance vascular species in the early regeneration after felling and burning has led to reports that felling and burning (CBS) is 'floristically benign' in *E. obliqua* wet forests in Tasmania (Neyland *et al.* 2009a).

The response of the cryptogam flora in wet sclerophyll forest was very different. After the most severe disturbance regime (felling and burning), transient early colonisers and disturbance species dominated, and the number of species characterising mature wet forest was very reduced and represented by small, widely scattered individuals. Five years after disturbance, the results suggest that recovery is likely to be extremely slow, over many decades (see also Turner and Kirkpatrick 2009; Browning *et al.* 2010). The vast majority of forest cryptogams will not re-establish until appropriate habitats in suitable micro-environments are restored. A few species can utilise different habitats before and after logging and burning but such examples are uncommon (Kantvilas and Jarman 2006). A study of the epiphytes of *E. obliqua* (Kantvilas and Jarman 2004) indicated that many eucalypt specialists do not colonise small trees and their habitat requirements will not be met within the proposed 90-year rotation. These results are consistent with those from a broader study of bryophytes in Tasmania's wet forest (Turner and Pharo 2005) that indicated some species could be at risk of exclusion from wood production areas through a combination of habitat/substrate loss and unfavourable rotation times. Compared with vascular species in the same vegetation type (see above), the effect of felling and burning (CBS) on cryptogams cannot be considered benign.

In eucalypt forest with rainforest understoreys, the chances of a cryptogamic flora recovering within prescribed rotation times

can be predicted with more certainty. The dominant rainforest vascular species are slow-growing, with slow dispersal rates (Tabor *et al.* 2007), and few of them were present in the regenerating vegetation at Warra, at least in the early years after severe disturbance (Neyland and Jarman 2011). The vascular flora itself is unlikely to recover within the planned rotation time frame (Cunningham and Cremer 1965; Hickey 1994; Neyland and Jarman 2011), so the prognosis for recovery of cryptogams that depend on these plants and the microclimates they create is extremely poor.

Assessment of comparison measures

Three aspects of species richness using presence/absence data were used to evaluate floristic changes occurring after disturbance. The most useful and informative of these involved classifying the species into ecological groups (Kantvilas and Jarman 2012). The approach indicated where losses and gains occurred in the flora and the magnitude of those changes. It was also sufficiently sensitive to respond to different levels and types of disturbance. A further refinement to include some measure of abundance (frequency and/or cover) would greatly improve results.

A second measure involved a comparison of which species occurred before and after disturbance. While this approach was able to signal the presence of significant changes in the flora, it provided little detail about the nature of the changes.

The third measure involved species richness only, with no qualifying information. This gave a misleading impression of the impact of disturbance on the lichen and moss flora. With the mosses in particular, the data suggested that the flora was relatively unchanged before and after disturbance (Fig. 6b). In the lichens (Fig. 6a), there was some reduction in species richness but species numbers were not significantly different from those in the pre-disturbance vegetation. However, an examination of both Figures 7 and 8 indicated that very critical changes had occurred in the flora. In the liverworts, there were few newcomers after disturbance to bolster species numbers, so a comparison of total species richness before and after disturbance more closely reflected the severity of species losses from the pre-harvest flora.

Concluding remarks

Managing the impacts of disturbance in the forest environment is critical for the sustainable use of production forests. In Tasmania, cryptogams (lichens, mosses and liverworts) constitute by far the greatest component of plant biodiversity in these forests. Their responses to disturbance differ from those of vascular plants, and their potential as sensitive ecological indicators is well-documented. An understanding of how these organisms respond to the specific disturbances of felling and burning, the two main factors that govern silvicultural activities in Tasmanian wet sclerophyll forests, is a major step towards utilising their potential as indicators in assessing the relative impacts of different silvicultural treatments on the biota.

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