Successional patterns of terrestrial bryophytes along a wildfire chronosequence in the wet eucalypt forests of southern Tasmania

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Abstract

Terrestrial bryophytes are a major component of wet eucalypt forests and can often outnumber vascular species in terms of diversity. This study compared ten sites along a wildfire chronosequence in southern Tasmania to determine whether bryophyte total cover and species richness were correlated with forest age (time since fire). Five different age-classes were selected, each defined by the number of years since a stand-replacing fire event: last burnt before 1896 (>110 years), and last burnt in 1898 (108 years), 1934 (72 years), 1967 (39 years) and 2005 (1 year). Forest age was significantly correlated with species richness of terrestrial bryophytes, and species composition was significantly different between the different forest age-classes.

Introduction

Wet eucalypt forests form a significant component of the vegetation in Tasmania. This type of forest occurs in areas characterised by high rainfall and rich soils (Wells and Hickey 1999), and relies on large-scale disturbance, principally wildfire, for regeneration. In the absence of wildfire, wet eucalypt forests have a limited lifespan of approximately 400 years, ultimately giving way to cool-temperate rainforest (Wells and Hickey 1999). Wet eucalypt forests have considerable economic value in Tasmania as they comprise the majority of production forests, and are also an important source of biodiversity (Hickey 1994). Within these forests, terrestrial bryophytes are a significant contributor to biodiversity and often outnumber vascular species (Jarman and Kantvilas 1994; Pharo and Blanks 2000). Further, bryophytes may be functionally important. For example, studies in other forest types have shown moss beds to be important for vascular plant germination and survival, moisture relations, and nutrient cycling (Allen 1987; Nakamura 1992).

There have been numerous studies of the vascular flora in the wet eucalypt forests of Australia, though few studies have focused upon bryophytes (Hickey 1994; Lindenmayer 1995; Lindenmayer and McCarthy 2002). Studies to date have examined the effects on bryophyte diversity and abundance of differences in disturbance type (wildfire and logging) (Jarman and Kantvilas 2001; Turner 2003), the dynamics of initial post-fire colonisation (Duncan and Dalton 1982), and compared riparian and up-slope environments (Pharo and Blanks 2000); there has been little published work on the specific influence of forest age.

Studies in the boreal forests of the northern hemisphere have shown forest age to have a direct influence upon bryophyte richness (e.g. Gustafsson and Hallingbaeck 1988). A similar phenomenon may occur in the wet eucalypt forests of Tasmania. Following a stand-replacing fire, wet eucalypt forests progress through several distinct phases of succession (Jackson 1968). Duncan and Dalton (1982) have shown that distinct phases in bryophyte succession exist during the initial period of post-fire re-colonisation, so it is possible that bryophytes within wet eucalypt forests also increase in diversity with forest age.

The aim of this study was to examine the successional patterns of terrestrial bryophytes over a wildfire chronosequence, and determine if bryophyte total cover and species richness increase with time since the last fire. As this is a preliminary study, the results presented here are intended as a basis for further research. This study complements other research aimed towards understanding the stand structure and floristic attributes of vascular species in Tasmanian wet eucalypt forests along a wildfire chronosequence (Turner *et al.* 2007).

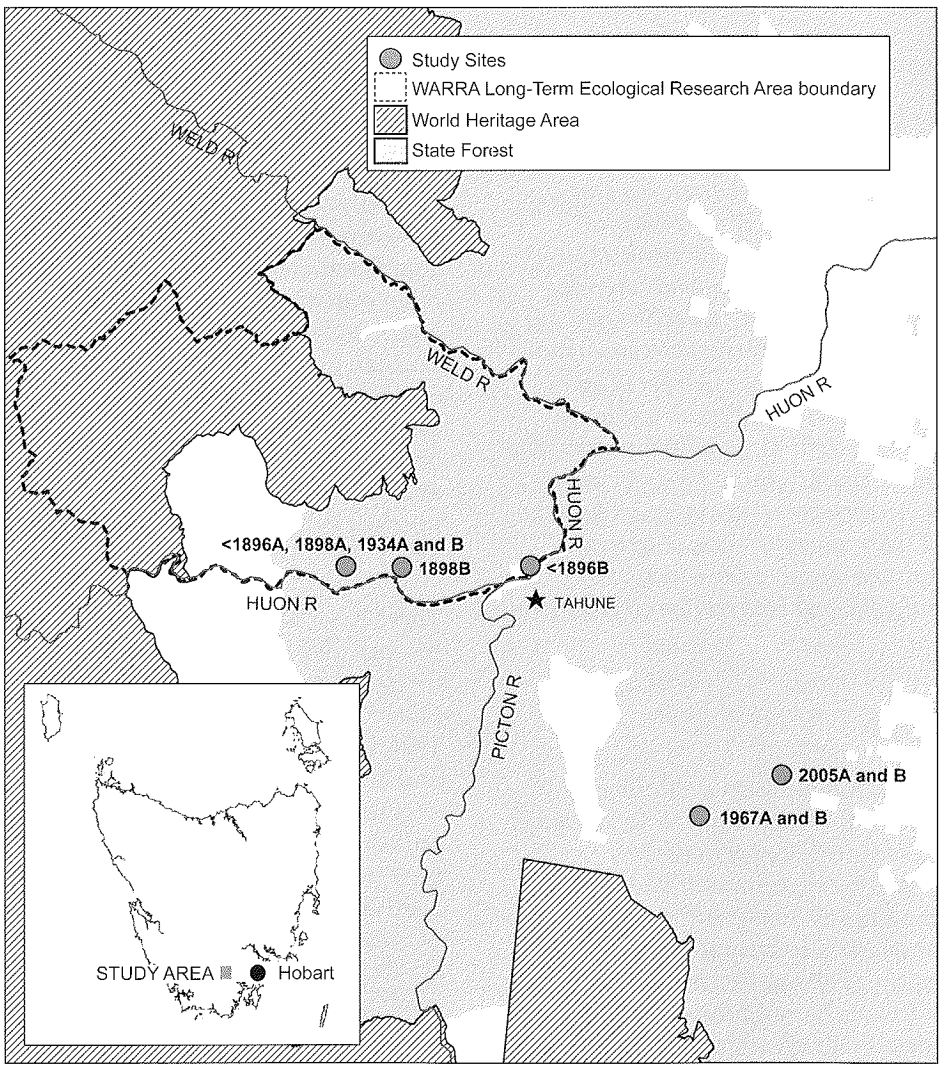


Figure 1. Location of the study sites.

Table 1. Summary of site characteristics.

Site	Geology	Vegetation
<1896A	Dolomite mixed with colluvial deposits of Jurassic dolerite	*E. obliqua* mixed forest with a *Nothofagus cunninghamii, Atherosperma moschatum* understorey over a ground layer dominated by *Dicksonia antarctica*
<1896B	Alluvial sands and gravel	*E. obliqua* mixed forest with a *Nothofagus cunninghamii, Atherosperma moschatum* understorey over a ground layer dominated by *Dicksonia antarctica*
1898A	Dolomite mixed with colluvial deposits of Jurassic dolerite	*E. obliqua* mixed forest with a *Nothofagus cunninghamii, Pomaderris apetala* understorey over a ground layer dominated by *Polystichum proliferum*
1898B	Jurassic dolerite	*E. obliqua* mixed forest with *Gahnia grandis, Melaleuca squarrosa* and *Bauera rubioides* understorey
1934A	Dolomite mixed with colluvial deposits of Jurassic dolerite	*E. obliqua* forest over *Nothofagus cunninghamii* and *Monotoca glauca* understorey over *Gahnia grandis* groundcover
1934B	Dolomite mixed with colluvial deposits of Jurassic dolerite	*E. obliqua* forest over *Nothofagus cunninghamii, Atherosperma moschatum, Pomaderris apetala* and *Anopterus glandulosus* understorey over *Gahnia grandis* groundcover
1967A	Jurassic dolerite	*E. obliqua* forest over *Phyllocladus aspleniifolius, Acacia verticillata, Monotoca glauca, Anopterus glandulosus, Nothofagus cunninghamii* and *Atherosperma moschatum* understorey over *Gahnia grandis* groundcover
1967B	Jurassic dolerite	*E. obliqua* forest over *Nothofagus cunninghamii* and *Atherosperma moschatum* understorey over *Dicksonia antarctica* groundcover
2005A	Jurassic dolerite	Burnt *E. obliqua* with epicormic shoots
2005B	Jurassic dolerite	Burnt *E. obliqua* with epicormic shoots over *Pteridium esculentum* and *Gahnia grandis* groundcover

Methods

Study area

The study was conducted in the southern forests of Tasmania, which extend from the Wellington Ranges to the Tasmanian World Heritage Area (Figure 1). Ten sites, representing five forest age-classes (two sites for each age-class), were selected (Table 1). Forest age-class was based on time since the last stand-replacing fire, that is, a natural wildfire or a regeneration burn subsequent to forest harvesting. Site fire history was derived from land-management records obtained from Forestry Tasmania. All sites shared the same southerly aspect and had *Eucalyptus obliqua* as the dominant canopy species. Geology (Laffan 2001; Forsythe *et al.* 2003) and understorey vegetation was assessed by the authors. Mean annual rainfall for the area is 1233 mm (Bureau of Meterology 2009), based on the nearest operational station (approximately 3.5 km from the study area, opened 1961) at the Tahune Reserve (elevation 75 m, 43.10 °S 146.73 °E).

Sampling

The two sites from the <1896 and 1898 age-classes were sampled in March/April 2006, and the remaining eight sites were sampled in July/August 2006. At each site, five 1 m x 1 m quadrats were placed randomly within a 50 m x 50 m plot. Within each quadrat, the percentage cover of rocks, leaf litter, coarse wood debris (>10 cm in diameter)

and bare ground were estimated visually using the Braun-Blanquet method (score 1 = 1-5% cover; score 2 = 5-25% cover; score 3 = 25-50% cover; score 4 = 50-75% cover; score 5 = >75% cover). This method was also used to score the percentage cover of bryophytes, including those on epiphytes that had fallen into the quadrat but excluding those occurring on rocks, coarse woody debris and trees. The number of bryophyte species (species richness) occurring in each quadrat was then recorded. Bryophyte species that could not be identified in the field were collected and identified in a laboratory using light microscopy (Scott and Stone 1976; Scott 1985; Meagher and Fuhrer 2003). Nomenclature follows Streimann and Klazenga (2002) for mosses and McCarthy (2003) for hepatics (liverworts).

Data analysis

The Braun-Blanquet cover scores were converted to a single percentage value mid-way between the two range values, e.g. score 4, 25-50% cover, was converted to 37.5%. Quadrat values were then averaged for each site. Mean rock cover was always below 4% and thus not included in the subsequent analyses. Analysis of variance (ANOVA) was then used to test for differences in both total cover and species richness between the different forest age-classes.

Ordination was performed using multidimensional scaling (MDS, using PRIMER, Bray-Curtis similarity, 25 starts). Analysis of similarities (ANOSIM, using PRIMER) was used to test for differences in species composition between the forest age-classes. ANOSIM is a distribution-free analogue of one-way ANOVA that compares rank similarities within pre-selected groups to average rank similarities between groups. ANOSIM constructs a test statistic (R) that is close to 1 if there is a significant difference

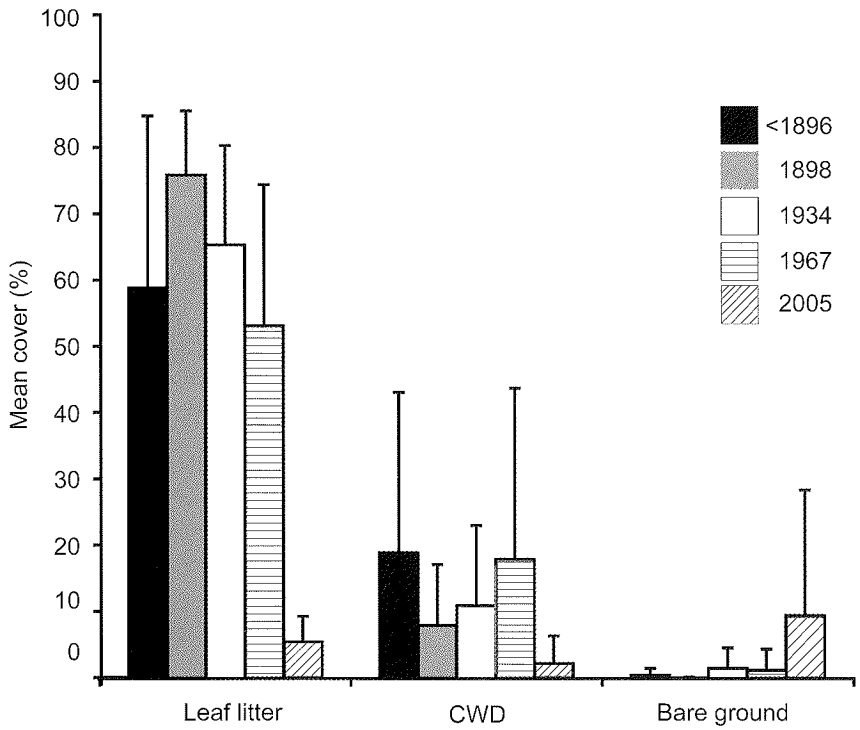


Figure 2. Mean ground cover of leaf litter, coarse woody debris (CWD) and bare ground in 1 m x 1 m quadrats at various sites (error bars represent stdev, n = 2).

in species composition within groups compared to between groups. If there is little difference within groups compared to between groups, then R is approximately 0 (Clarke 1993). Values of R were generated using 999 random permutations of the original groups.

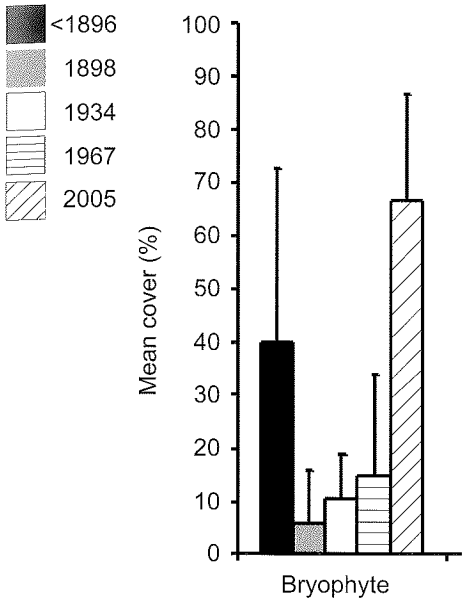


Figure 3. Mean bryophyte cover (error bars represent stdev, n = 2).

Results

Ground cover

At the two sites from the 2005 age-class, the total cover values for leaf litter (mean = 5.5%, stdev = 3.9%) and coarse wood debris (mean = 2.3%, stdev = 4.2%) were much lower than for the remaining sites (Figure 2). There was a significant difference in leaf litter cover between the five forest age-class (F = 25.68, df = 4, P <0.001).

Bryophyte cover and species richness

The 2005 age-class was different to the other age-classes in that the total cover of bryophytes (Figure 3) was much higher than that recorded for the remaining age-classes (mean = 66.5%, stdev = 29.9%). Bryophyte cover for the 2005 age-class was significantly higher than all the other age-classes when compared individually (Figure 3; e.g. <1896

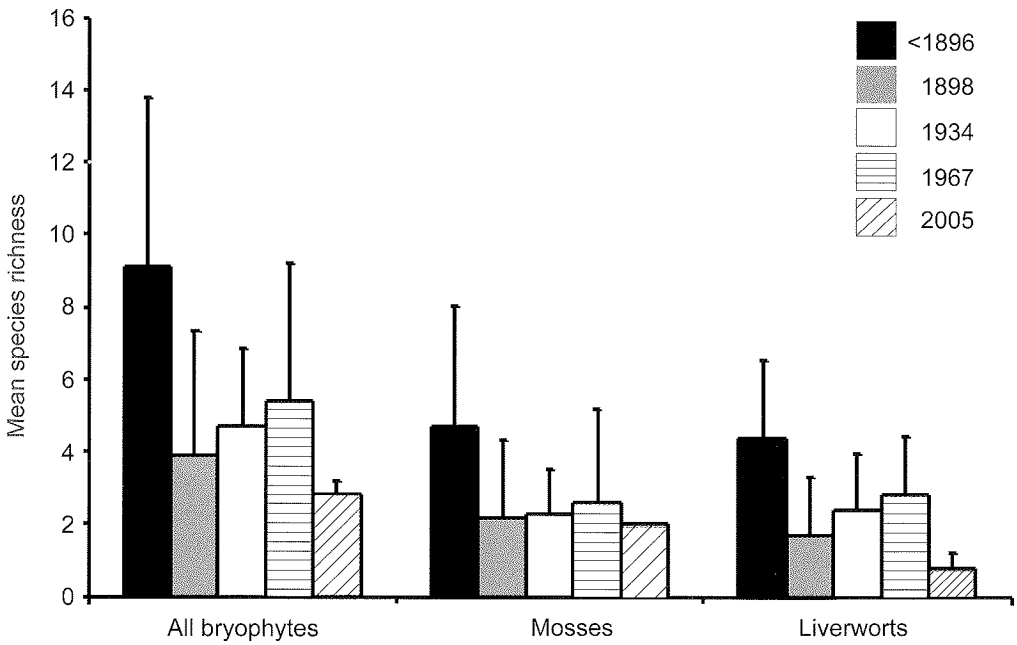


Figure 4. Mean species richness; all bryophytes, and mosses and liverworts separately (error bars represent stdev, n = 2).

age-class versus 2005 age-class, F = 4.67, df = 1, P = 0.044). Total cover of bryophytes was significantly higher for the <1896 and 2005 age-classes compared to the 1898, 1934 and 1967 age-classes (F = 25.68, df = 4, P <0.001).

A total of 42 bryophyte species (21 mosses and 21 liverworts) were recorded across the 50 quadrats (Appendix 1). Bryophyte species richness (Figure 4) was significantly related to forest age-class (F = 5.36, df = 4, P <0.001), where the <1896 age-class had the highest mean species richness (mean of 9.1 species per 1 m x 1 m quadrat) and the 2005 age-class had the lowest mean species richness (mean of 2.8 species per 1 m x 1 m quadrat). Species richness was significantly greater for the <1896 age-class compared to the other age-classes (<1896 compared to 1898, F = 9.04, df = 1, P = 0.008; <1896 compared to 1934, F = 6.97, df = 1, P = 0.017; <1896 compared to 1967, F = 4.75, df = 1, P = 0.043; <1896 compared to 2005, F = 17.50, df = 1, P <0.001). Based on the pairwise difference, species richness of the 1967 age-class was close to being significantly different to that of the 2005 age-class (F = 3.73, df =1, P = 0.067). No significant differences were found in species richness among the 1967, 1934 and 1898 age-classes.

Species composition

Ordination (not shown) demonstrated two distinct groups of age-classes, with the two sites from the 2005 age-class plotting together and the eight sites from the other age-classes plotting closer to each together (stress = 0.01; Global R = 0.598, P <0.001). The 2005 age-class was thus significantly different to all other forest age-classes in species composition. Three species (*Ceratodon purpureus, Funaria hygrometrica* and *Marchantia berteroana*) were found exclusively at sites from the 2005 age-class, and represented the entire bryoflora for this class. When analyses were re-run without the 2005 age-class, the global R value dropped to 0.195 but there was still a significant difference overall in species composition between sites (P <0.001). This difference was determined by differences in species between some of the intermediate age-classes (1934 compared to 1967, R = 0.306, P <0.001; 1898 compared to 1934, R = 0.254, P = 0.005). Despite these differences, several species were common to these four older age-classes: *Bazzania adnexa, Dicranoloma billarderi, Heteroscyphus fissistipus, Hypnodendron comosum, Ptychomnion aciculare* and *Teleranea patentissima* all occurred within each of the older four age-classes.

Discussion

This study contributes baseline information on bryophytes to one of Warra LTER icon projects, the wildfire chronosequence study. The overall result was a strong contrast between the recently burned forest (2005 age-class) and the other age-classes, with sites from the 2005 age-class containing a high cover of three pioneer, disturbance-adapted species not found at the older sites.

Ground cover

The character of leaf litter changed between each of the forest age-classes, with a change in the type (data not shown) and amount of leaf litter presumably caused by the changing composition of forest canopy species. This pattern could be seen when the 1898 age-class was compared with the <1896 age-class; as the eucalypt species senesced, the depth and amount of leaf litter present decreased, which possibly provided a more stable habitat for bryophyte colonies. A reduction in eucalypt leaf litter may also provide a more favourable environment for bryophyte species as it would reduce any possible alleopathic effects of the tannins present in the eucalypt leaves. Environmental data being collected at these sites will be used to better understand bryophyte response to changing forest structure and composition.

Substrate is an important variable that can change over time and subsequently

influence bryophyte diversity (see Bates, 2000 for a review), though an investigation of this was beyond the scope of this study. The influence of substrate on both total cover and species richness warrants further investigation.

Bryophyte cover and species richness

There was a significant difference in the total cover of bryophytes between the forest age-classes. This was possibly due to the differences in forest character between the 2005 age-class and older forest age-classes. The recent fire (2005 age-class) had largely removed the forest canopy, greatly reduced the leaf litter, and cleared the understorey and groundcover strata. This would provide a high-light, high-nutrient environment more suitable for pioneer bryophyte species.

In terms of species richness, there was a strong contrast between the species-poor youngest age-class (2005) and the species-rich older sites, in particular those from the <1896 age-class. The <1896 age-class was significantly more species-rich than each of the other age-classes. However, the three intermediate age-classes, 1898, 1934 and 1967, showed a reverse but non-significant trend of decreasing species richness with age, although with greater replication a different relationship between age and terrestrial bryophyte richness might emerge. Forest age may thus not be a dominant factor in intermediate-aged forests, and environmental variation not related to age, for example proximity to watercourses, might play an important role in the number of terrestrial bryophyte species in forests of intermediate ages.

Species composition

There was a highly significant difference in terrestrial bryophyte species composition among the forest age-classes, due largely to the difference in species composition between the 2005 age-class and the other four age-classes. When the 2005 age-class data were excluded from the analyses, there was less distinction in species composition, although a few species occurred only in a specific age-class. The complete turnover of species between the 2005 and 1967 age-classes, and the ongoing changes and accumulation of species into the <1896 age-class, were consistent with previous descriptions of post-fire re-colonisation both in Tasmania (Duncan and Dalton 1982) and overseas (Brasell & Mattay 1984; Thomas *et al.* 1994; Weber and van Cleve 1984). In contrast to the recently burnt sites, the <1896 age-class forest presumably provided a more humid, heterogeneous environment, and consequently a wider range of habitats for a greater range of bryophyte species. Alternatively, as the <1896 age-class forest had the longest disturbance-free period of all the age-classes studied, it also provided the greatest amount of time for species to colonise and become established. The distinctiveness of the <1896 age-class is thus consistent with a slow successional sequence of bryophytes in wet eucalypt forests, with some species particularly slow to disperse and establish into disturbed areas. Recent experimental evidence from both bryophyte and lichen studies suggests that many bryophyte species are more dispersal-limited than has previously been acknowledged (see Pharo and Zartman 2007 for a review). Some species may thus be disturbance-limited, while the microhabitat conditions necessary for other species may not develop for more than 100 years.

There are a wide range of life-history strategies among bryophytes, and using species attributes to understand the nature of disturbance is a useful approach (e.g. Johansson *et al.* 2006). Some species were restricted to the 2005 age-class, whereas a number of other species were present in all but the recently disturbed sites. The latter species may have been responding to the availability of similar microhabitats at all but the most recently disturbed sites, or perhaps their distribution reflected adaptable life history strategies.

More work is needed to determine the most important limiting factors, and the variability of these factors between species.

Conclusion

The study collected preliminary data on the influence of forest age on terrestrial bryophyte species diversity and total cover within wet eucalypt forests. The data show that forest age has an influence on bryophyte diversity, and that, while older forests have the greatest bryophyte diversity, the role of younger forests and associated pioneer/ successional species is also important.

There is not a simple relationship between terrestrial bryophyte diversity and age, and more data are needed to better understand the role of forest age and substrate on bryophyte diversity, particularly during the first 40 years following fire.

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